

Radula subg. *Radula* in Australasia and the Pacific (Jungermannniopsida)

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Abstract

Seven species belonging to *Radula* subg. *Radula* are accepted for Australasia. *Radula oreopsis* M.A.M. Renner is described as new, while *R. kurzii*, *R. multiflora*, *R. reflexa* and *R. sharpii* are excluded from the region. Molecular and morphological data provide evidence suggesting that the broad species concepts recently applied to subg. *Radula* in Australia and across the Pacific are not useful. Many subtle yet consistent differences in size and shape, and in micromorphological and anatomical characters potentially inform species circumscription. However, most differences between species are virtually impossible to apprehend independent of molecular data corroborating their significance. Herbarium-based studies and the interpretation of type material are therefore challenging. However, the molecular phylogeny based on three chloroplast markers unites a morphologically heterogeneous array of individuals from across Australasia and the Pacific into a single fully supported clade containing individuals corresponding to the type of *R. javanica* as well as individuals from Australia, New Zealand and Fiji attributed by various workers to *R. erigens*, *R. javanica*, *R. multiflora* and *R. reflexa*. There is a general lack of congruence between morphological and molecular groups across the phylogeny. Morphologically similar individuals are resolved in different clades where they are more closely related to morphologically dissimilar species, which may hint at morphological convergence. Morphologically different individuals are nested within each other. The unique cell ornamentation in *R. oreopsis*, but not in other individuals (here attributed to other species) within the same clade is one example hinting at rapid morphological evolution. The dispersed nature of land within island archipelagos means spatial isolation could contribute to origin and maintenance of species diversity across the Pacific. Every habitat may be effectively peripherally isolated by dispersal limitation. If rates of dispersal and divergence are equivalent across the region, the Pacific and bounding lands including the Wet Tropics Bioregion could maintain species paraphyly in perpetuity.

Introduction

The first subdivision of *Radula* was by Spruce (1884) who proposed subgenus *Cladoradula* Spruce for one species with spherical capsules and no subfloral innovations, the remaining 12 Amazonian and Andean taxa he placed into subg. *Radula*. Almost simultaneously, Stephani (1884) conceived 12 artificial sections as an aid to species identification. Castle (1936) combined Spruces subgeneric scheme with Stephani's sections at a time when evolutionary systematic thought should have been exerting a strong influence on the supra-specific classifications throughout the Hepaticae. Jones (1977) articulated a scathing critique of the sectional subdivision of *Radula* adopted by Castle but made no taxonomic changes. Two years later, Yamada (1979) segregated from subg. *Radula* species with acute leaf-lobe apices and two pairs of female bracts between the subfloral innovations and the perianth base, and placed these into subg. *Odontoradula* K. Yamada. Schuster (1980), after nearly three decades of revisionary study on liverwort classification finally brought himself to

publish one of his two papers treating the Radulaceae, a family he regarded as interesting as *Bazzania* in its morphological monotony (though to his credit he published even fewer papers on *Bazzania*). Schuster (1980) identified in species of *Radula* subg. *Odontoradula* and in some species of subg. *Radula* the presence of what he called an *Isotachis*-type stem perigynium. The latter were removed to subg. *Metaradula* R.M.Schust. as he regarded the presence of a stem-perigynium as defining a fundamental division within *Radula* (Schuster 1980). He even mooted segregating subg. *Metaradula* and subg. *Odontoradula* into a separate genus on this basis (R.M.Schuster *pers. comm.* 2003). Unfortunately, Schuster's (1980) consideration of subg. *Radula* became bogged in the quagmire of pre-existing sectional, subsectional, and serial segregates. In the subgeneric classifications of both Yamada and Schuster subg. *Radula* comprised species not accommodated in any other subgenus. Unsurprisingly subg. *Radula* was found to be polyphyletic in the molecular phylogeny reconstructed by Devos et al. (2011a). The generitype, *Radula complanata* (L.) Dum. grouped with a number of morphologically similar species in a fully supported clade nested within another comprising a diverse suite of morphologically dissimilar species. This aggregation of morphologically disparate species in a monophylum was not unique, as subg. *Odontoradula* and subg. *Amentuloradula* also comprised assemblages of morphologically dissimilar species that had previously been attributed to different subgenera. High levels of morphological homoplasy were reflected in the high uncertainty associated with ancestral character state reconstructions for 20 characters previously employed in infrageneric classification of *Radula*. The broad morphological circumscriptions presented in the subgeneric classification revised by Devos et al. (2011b) reflected the lack of clade defining synapomorphies, at least among characters previously employed to define infrageneric groups.

In a preliminary treatment of the Queensland species of *Radula*, Yamada (1987) identified 16 species belonging to subg. *Radula*; however, all but six belong in other subgenera (Table 1). Preliminary analyses including *R. patens* K.Yamada are inconclusive as regards subgeneric affinities; however the species is not a member of subg. *Radula* (M.A.M.Renner unpublished data). The subgeneric placement of *R. patens* and its close relatives will be the subject of a subsequent contribution.

Table 1. Australian species assigned to subg. *Radula* by Yamada (1987) with their current subgeneric placement (where known) and notes on their status in Australia

Species	Subgenus	Notes
<i>R. acutiloba</i>	<i>Radula</i>	
<i>R. hicksiae</i>	<i>Amentuloradula</i>	
<i>R. javanica</i>	<i>Radula</i>	
<i>R. jovetiana</i>	<i>Metaradula</i>	
<i>R. kurzii</i>	Unassigned	Excluded from Australia
<i>R. loriana</i>	<i>Metaradula</i>	
<i>R. multiflora</i>	(?) <i>Radula</i>	Excluded from Australia
<i>R. nymanii</i>	<i>Metaradula</i>	
<i>R. parvitexta</i>	<i>Metaradula</i>	Synonym of <i>R. robinsonii</i>
<i>R. patens</i>	Unassigned	
<i>R. reflexa</i>	(?) <i>Radula</i>	Excluded from Australia
<i>R. retroflexa</i>	<i>Odontoradula</i>	
<i>R. sharpii</i>	(?) <i>Radula</i>	Excluded from Australia
<i>R. tasmanica</i>	<i>Odontoradula</i>	
<i>R. thiersiae</i>	<i>Amentuloradula</i>	

Radula acutiloba Steph. was described as a new species from Australia by Stephani (1889) on material collected by F.M. Bailey in Queensland. A similar plant from New Zealand, collected by W. Colenso, was described as *R. papulosa* Steph. (Stephani 1892). *Radula papulosa* was synonymised with *R. acutiloba* by Yamada (1987), and this was followed by So (2005), but not by Meagher and Fuhrer (2003) or Renner (2005).

Radula javanica was first reported for Australia by Stephani (1889). In his revision of south-east Asian *Radula*, Yamada (1979) described *R. javanica* as one of the most plastic species, being highly variable in both the size and shape of leaf-lobes and lobules; and again in his treatment of Queensland species he described Australian *R. javanica* as being highly variable in forms of leaf-lobes and lobules (Yamada 1987). Broad ecological variation was reported for *R. javanica* by Yamada and Piippo (1989), which had an altitudinal range on the Huon Peninsula (Morobe Province) of Papua New Guinea of 40–2500 m asl. The circumscription of

R. javanica has been progressively broadened since Castle's (1966) treatment in his worldwide revision, as has the reported range of *R. javanica*. Castle (1966) listed no synonyms, while Yamada (1979) listed seven synonyms. In her synopsis of *Radula* in the South Pacific, So (2006) included ten species in the synonymy of *R. javanica*, including four newly proposed. Among these were several having type specimens from the Pacific, including *Radula oceania* Castle, *Radula cordiloba* Taylor, *Radula subpallens* Steph. ex Besch., *Radula unduliflora* Castle, several more having types in New Caledonia, and two with types in Melanesia. Morphological variation within individuals, broad similarity between individuals, and ecological similarities were cited as justification for further broadening the circumscription of *R. javanica* (So 2006). *Radula javanica* has also been reported from the neotropics (Yamada 2000).

Radula kurzii Steph. was reported new for Australia by Yamada (1984). The type was collected from the Andaman Islands. This species was regarded as synonym of *R. javanica* by Miller et al. (1983).

Radula sharpii K.Yamada was described from Papua New Guinea by Yamada (1985) and reported for Queensland by Yamada (1987) on a specimen collected by Ilma Stone in Mossman Gorge.

At the end of Die Gattung *Radula*, Stephani (1884) noted that Ferdinand von Mueller in *Fragmenta Phytographiae Australiae* (Mueller 1878–1881) discussed two plants which he called *Radula gottscheana*, one from Rockingham Bay, the other from Keppel Bay. Stephani saw the former and considered it *R. reflexa*, the first report of this species from Australia. Stephani (1889) subsequently reported *R. reflexa* for Norfolk Island, which Yamada (1979) regarded as doubtful. Yamada (1987) reported Australian collections of *R. reflexa* from Cape Tribulation made by M.L. Hicks. *Radula reflexa* was reported for Fiji, New Caledonia and Tahiti, and types of synonyms from Indonesia and Hawaii were given, resulting in a range extending from Borneo eastward across Melanesia through Papua New Guinea, Australia, and across the Pacific to Hawaii (So 2006).

All records described above have been based on morphological data. Lobule characters in particular are central to species circumscription within *Radula*, and distinctive or unusual lobule characters have been identified as diagnostic of many species. Some species have been named for lobule characters, such as *Radula voluta* from the northern hemisphere, while *R. acutiloba*, *R. retroflexa* and *R. reflexa* are local examples. The lobules of *Radula reflexa*, as the specific epithet suggests, are reflexed in their upper half, and a number of different species have been proposed for the range of plants expressing lobules reflexed to varying degrees. So (2006) accepted only two of these for the Pacific, she expressed some hesitation in retaining *R. decurrens* Mitt. and *R. reflexa* as distinct species, the former differing in its undulate leaf-lobe margin. Everything else with reflexed lobules So (2006) treated as *R. reflexa*. Yamada (1979) regarded the subquadrate or rhombic leaf-lobules, often strongly recurved from the upper 2/3 of adaxial margin to the apex, as diagnostic of *R. reflexa*. He also alluded to similarities between this species and *R. multiflora* (also having an Indonesian type) but noted that *R. multiflora* was distinctive in its flat lobule apex, but recurved basal margin. Plants from Queensland with these features were the basis for Yamada's (1984) Australian record of *R. multiflora*. As noted above, Yamada (1979, 1987) regarded *R. javanica* as variable but described and illustrated plants with flat lobules, lacking reflexed or recurved margins or apices. Although So (2006) followed Yamada's circumscription of *R. reflexa*, she placed *R. multiflora* in synonymy of *R. javanica*, expanding this already variable species to include plants with recurved as well as flat basal lobule margins.

The purpose of this study is to identify species of *Radula* subg. *Radula* in Australia. For comparative purposes samples from across the Pacific were included to assist in establishing parameters and limits of variation expressed by, and relationships between, Australian species of this subgenus.

This study is the product of an ABRIS Postdoctoral Fellowship with the Royal Botanic Gardens and Domain Trust upon which Elizabeth Brown was joint investigator. Much of the material included in the molecular component of this study was collected in her company, during fieldwork in some magnificent and fascinating landscapes throughout Australia and Fiji. It is sad that Elizabeth did not live to capitalize on the opportunities generated by this fieldwork. This study reaches conclusions about species circumscription and nomenclature that Elizabeth would probably have found unsatisfactory in their incompleteness, and their lack of consistency with molecular evidence. However, she appreciated the world was often more complex than expected, and that you just have to do your best when dealing with difficult plants. This study is dedicated to her.

Methods

Taxon sampling and molecular protocols.

Sampling for DNA was based on material collected throughout the Australasian geographical ranges reported for *R. javanica* and *R. reflexa*, and other species of subg. *Radula*. At each site one to five collections representing the morphological and ecological diversity exhibited by each species were made. The objective of sampling was to include multiple individuals of each morphological type from many sites across their distributions. Clean shoot tips comprising the meristem, embryonic leaves, and one or two nearly mature leaves were excised from each specimen until approximately 25–50 mm² of cleaned material was obtained, depending on plant size. Study specimens were either stored on silica gel or rapidly air dried from wild collected material to ensure plant material remained green and free of fungus.

Total genomic DNA was extracted using the DNeasy Plant Minikit (QIAGEN Pty Ltd, Sydney Australia). Three chloroplast markers were sequenced, (1) the *atpB-rbcL* spacer, (2) the plastid *trnL-F* region including the *trnL(UAA)* group1 intron and the *trnL-F* intergenic spacer, hereafter *trnL-F*, and (3) the *trnG* G2 intron. These three markers were selected due to higher success at obtaining clean PCR product for chloroplast than nuclear markers, and these three regions evolve quickly enough to acquire synapomorphies indicative of reproductively isolated groups. Primer details are presented in Table 2. Polymerase chain reaction (PCR) was carried out using the following protocols. For *trnL-F* each 15 µl reaction contained 1.5 µl 10× PCR Buffer, 1.5 µl 20 mM MgCl₂, 0.9 µl of each primer at 10 µM concentration, 0.12 µl of 1% BSA, and 0.12 µl of Immolase Taq. For the *atpB-rbcL* and *trnG* each 15 µl reaction contained 1.5 µl 10× PCR Buffer, 0.75 µl 20 mM MgCl₂, 0.9 µl of each primer at 10 µM concentration, 0.12 µl of 1% BSA, and 0.08 µl of Immolase Taq. Temperature profile used for sequencing was 95° C for 10 minutes, then 35 cycles of 95° C for 1 min, 1 min at annealing temperature of 53° C for *trnL-F* and *trnG*, and 50° C for *atpB-rbcL*, then 72° C for 1 min, followed by a final extension step of 72° C for 10 min. The same primers were used for sequencing of cleaned PCR products by Macrogen Inc., South Korea (<http://www.macrogen.com>).

Table 2. Primer Details

Region	Primer	Sequence 5'-3'	Direction	References
atpB-rbcL	atpB-1	ACATCKARTACKGGACCAATAA	Forward	Chiang et al. (1998)
	rbcL-1	AACACCAGCTTTAATCCAA	Reverse	Chiang et al. (1998)
trnL-trnF	A50272	ATTGAACTGGTGACACGAG	Forward	Taberlet et al. (1991)
	B49317	CGAAATCGGTAGACGCTACG	Reverse	Taberlet et al. (1991)
trnG	trnGF	ACCCGCATCGTTAGCTTG	Forward	Pacak & Szweykowska-Kulinska (2000)
	trnGR	GCGGGTATAGTTAGTGG	Reverse	Pacak & Szweykowska-Kulinska (2000)

DNA sequence alignment and Phylogenetic analyses.

For each DNA region, forward (5' -3') and reverse (3' -5') sequences were assembled and checked for inaccurate base calling using Geneious (Drummond et al. 2012). Consensus sequences were aligned by MUSCLE (Edgar, 2004) on the CIPRES portal (Miller et al. 2010) and manually edited in BioEdit 5.0.9 (Hall 1999) following alignment rules and principals of homology outlined in Kelchner (2000) and Morrison (2006).

Ultrametric trees summarising relationships and relative divergence times were estimated using the Bayesian software BEAST version 1.4.8 (Drummond & Rambaut 2007). Three partitions with unlinked GTR + I + Γ substitution models were specified. Base frequencies were estimated from data, gamma had six categories, and all substitution models and clock models were unlinked. Substitution model priors followed default settings in BEAUTi v.1.7.2. A separate uncorrelated lognormal relaxed-clock modelled substitution rates for each partition, with rates estimated relative to *atpB-rbcL*. A uniform prior with range 0–100 was applied to

each clock, a speciation birth-death model (Gernhard 2008) with a uniform distribution applied to node heights, and an unweighted pair-group mean aggregate (UPGMA) dendrogram was used as the starting tree. Phylogeny was not time-calibrated, however branches in resulting ultrametric trees are proportional to time. The analysis was run for 19.8 million generations (the number completed in a 24 hour period) and sampled every 1000. Burnin length and convergence between the four runs were confirmed by comparing trace files for each run in Tracer v.1.5 (Rambaut & Drummond 2009). After excluding the first 10% of samples as burnin, the 50% majority rule tree summarised the sampled trees.

Morphology

Specimens of *Radula* from AK, BM, BRI, CANB, CHR, FH, G, MEL, MPN, NSW, NY, S, and WELT, were examined. The distribution of the specimens examined is summarized according to subregions of Papua New Guinea (Womersley 1978), and those of Australia according to the regions of Queensland (Anonymous 1975) and New South Wales (Anderson 1961; Jacobs and Pickard 1981). The distribution of specimens for other countries are summarised according to official standardised geographical island groups.

Morphology was assessed with the aid of dissecting and compound microscopes. In the descriptions, measurements are given for the smallest and largest observed values for a given structure, so are indicative of range only. Leaf lobe length defined as perpendicular to the stem axis, width parallel to the axis, and not including the lobule. When assessing lobule shape it was necessary to rehydrate and slide mount material for investigation with a compound microscope.

Stem transverse sections were prepared by hand from primary shoots, with sections taken from three different shoots for each individual, and slide mounted in water for observation. Dissections of female bracts, gynoecia, and archegonia were by hand and slide mounted in water. Longitudinal sections of the perianth were also prepared by hand, with two or three perianths from a selection of individuals examined for each species depending on availability, and slide mounted in water.

Observations of species ecology were made during fieldwork in Fiji and Australia between 2008 and 2013.

Results

Sampling

Seventy-five individuals of *Radula* subg. *Radula* were sampled (Table 1), and sequences obtained from all 75 for *atpβ-rbcL* spacer and *trnL-F*, and from 69 for *trnG* (Table 1). A further 92 individuals sampled in the global phylogeny by Devos et al. (2011a, b) were included (see Renner et al. 2013a for details). Alignments resulted in datasets of 666 putatively homologous sites for *atpβ-rbcL* spacer (647 uninformative and 19 parsimony informative characters); 778 putatively homologous sites for *trnG* (539 uninformative and 239 parsimony informative characters); and 642 putatively homologous sites for *trnL-F* (488 uninformative and 154 parsimony informative characters). The concatenated dataset included 2086 sites, of which 412 were parsimony informative, and included 363 of the total 495 sequences, a missing rate of 27%, most of which were in the *atpβ-rbcL* spacer region.

Phylogenetic analysis

All data partitions converged on compatible topologies for supported clades, with no significant disagreement. For the concatenated data 19,840 trees were sampled from the posterior probability distribution by BEAST, and the first 1984 were excluded as burnin.

In the estimated phylogeny (Fig. 1), 88 terminals were resolved within a clade corresponding to *Radula* subg. *Radula* with full support. The basal bifurcation yielded two clades, one strongly supported containing 10 terminals, including the generitype *R. complanata* (in clade G); the other not supported containing the remaining 78 individuals (including clades B–F). In clade G three individuals of *Radula acutiloba* (Figs 2–4) were resolved paraphyletic but without support at the base of the clade.

Sister to G this was a fully supported clade containing several strongly or fully supported monophyla whose relationships were unresolved. Several of these monophyla corresponded to morphological entities.

Radula mittenii Steph. (clade F) was resolved with full support. This species was treated by Renner et al. (2013a) as part of the *R. buccinifera* complex.

In clade E eleven individuals from Fiji were resolved in a strongly supported clade that shared three distinctive features: the lobules on primary shoots have the antical margin reflexed on line perpendicular to stem, and interior margin reflexed on line parallel with the stem; the leaf lobes are almost rectangular in outline;

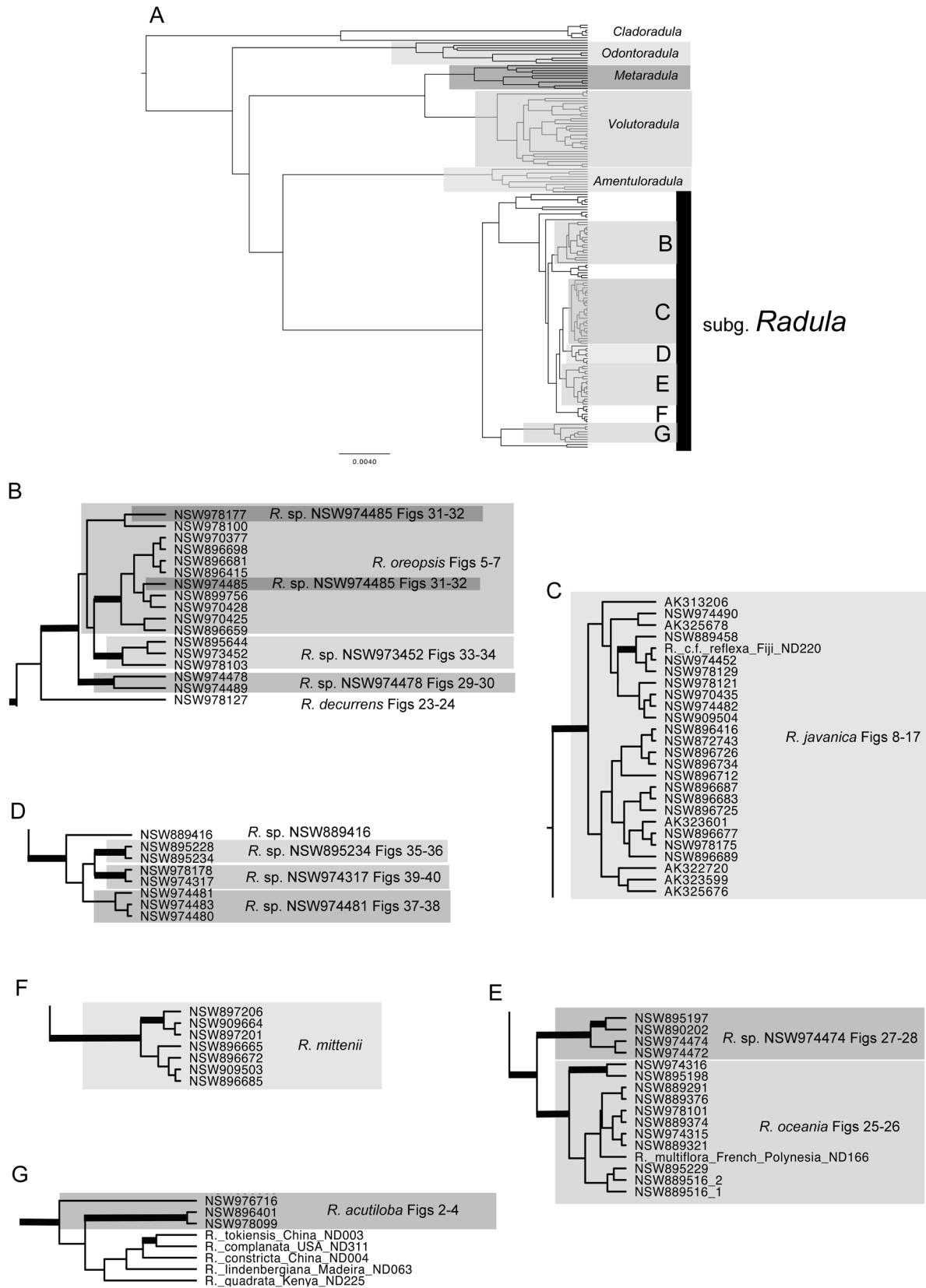


Fig. 1. Fifty percent majority rule consensus of trees sampled from posterior probability distribution by BEAST, node heights are medians from 17856 sampled trees after removing burn in. Letters correspond to clades containing Australasian and Pacific species of subgenus *Radula*. Bold branches indicate posterior probability ≥ 0.9 .

the margin of leaf-lobes on secondary shoots are inrolled and the marginal cells overlap adjacent cells in ventral view (Figs 25, 26). Female bracts are imbricate, with elliptic-reniform lobules half the area of the lobe on the inner-most bract. An individual identified as *R. multiflora* in the phylogeny of Devos et al. (2011a, b) was included in this clade which shares characters with Castle's *Radula oceania* (Castle 1965), whose type is from Samoa, including the reflexed leaf-lobe margin on 'branches'. This name is adopted for this clade, though further investigation of the type material is required to confirm the accuracy of this application. In a supported sister relationship with *R. oceania* is a fully supported monophylum comprised of four individuals from Vanuatu and Fiji, distinctive in the imbricate, ampliate lobules on primary shoots lobules that have the apex turned outward away from the stem; in the primary and secondary shoot lobules having no reflexed margins, and in the ovate leaf-lobes, whose margins on secondary shoots are inflexed; and in the absence of caducous leaf-lobes (Figs 27, 28). No species name was resolved for this clade here referred to as *R. sp.* NSW974474.

Sister to clade E (*R. oceania* and *R. sp.* NSW974474) is a supported clade comprising two fully supported subclades (clades C + D). Clade C (the larger within the context of our sampling) of these was fully supported, and contained 26 individuals of diverse form distributed from tropical Australia through the Pacific. Three forms are described below. Firstly, some individuals have leaf-lobes all caducous shortly after maturation, and the shoot systems are entirely devoid of leaf-lobes except at the apex of the shoots. Lobules are quadrate, and often have the entire free portion reflexed along a line between the antical end of the stem insertion and the lobe-lobule junction. Individuals with this morphology were collected in Australia and Fiji, as rheophytes (Figs 8–10). They did not group together in the phylogeny. The specimen included as *R. c.f. reflexa* in the phylogeny of Devos et al. (2011a,b) has the same morphology and was itself collected as a rheophyte in Fiji.

Another form in clade C, though not too dissimilar in detail is of rather different appearance due to the absence of reflexed lobules and reduced frequency of caducous leaf-lobes. Lobules in this form are reflexed along the antical margin only, and this corresponds to the lectotype of *R. javanica*. Individuals of this morphological form were collected in Australia and Fiji as epiphytes within forest (Figs 11–13). Again they did not group together in the phylogeny.

Another form in clade C has larger quadrate lobules with an ampliate interior margin that covers the stem, and may be reflexed along the interior margin only. Caducous leaves tend to be localised to secondary branches. Individuals with this form were collected in Australia, New Zealand, Vanuatu, Cook Islands as epiphytes and lithophytes within forest (Figs 14–16).

The smaller clade D (sister to clade C) comprised four morphological entities, two of which formed fully supported monophyla, although each was represented by only two individuals, another of which formed an unsupported monophylum, the fourth of which was represented by a single individual. These four morphological entities are described below.

Radula sp. NSW974481 is characterised by its large, plane, rhombiform lobules without reflexed margins, and crenulate leaf-lobe margins, pinnate branching, imbricate leaf-lobes. Three specimens from Vanuatu, all collected as epiphytes, were included in the analysis (Figs 37, 38). This morphotype corresponds to a monophylum without support (posterior probability = 0.87).

Radula sp. NSW895234 is characterised by nearly pseudo-dichotomously branched shoot systems whose branches are widely spaced, oblong lobules with reflexed interior margin, and apex adpressed against the leaf-lobe and stem, particularly when dry, the leaf-lobe margin is flat, and the contiguous leaf-lobes (Figs 35, 36). The two individuals in this clade were collected in Fiji as epiphytes in higher elevation forests where they grew as pendulous wefts from branches and tree-trunks within forest. They are not known to correspond with any type material.

Radula sp. NSW974317 bears some similarity to *R. oceania*. It has oblong leaf-lobes, rhomboid to oblong lobules whose interior margin is often reflexed, and whose apex may be reflexed along a line perpendicular to the stem. However, female bracts are not closely imbricate and with oblong-elliptic lobules up to one half the lobe area (Figs 39, 40). Margin of lobes on secondary shoots not inrolled, margin crenulated due to differential thickening of medial cell walls. Two specimens, both from the Fijian Island of Kadavu, were collected as epiphytes in low-mid elevation forest.

The fourth entity, *R. sp.* NSW889416 is apparently different in its flat leaf lobes with margin entire, and large oblong lobules with pronounced ampliate interior margin whose antical margin exceeds the lobule apex, are imbricate and obscure the stem in ventral view, and have the apex adpressed toward the leaf lobe such that the exterior margin has a shallow undulation (no figure). The sampled individual was collected as an epiphyte in mid-altitude forest on Viti Levu in Fiji, alongside individuals of *R. oceania*.

The remaining sampled individuals (17 in total) formed a strongly supported clade (B). Within the clade containing sampled individuals was a highly distinctive plant having closely imbricate leaf-lobes, and on primary shoots large rotund lobules whose reflexed interior margin still exceeds the opposing stem margin, and whose apex is reflexed along a curved line about half-way down the free portion that is lower on the interior than the exterior so that the curves alternate and appear to interlock on up primary shoots (Figs 23, 24). On secondary shoots the lobule interior and antical margins are reflexed but not to the same degree, and the leaf lobe margin is plane. In the leaf-lobe and lobule size and shape and in the pattern of lobule reflexion this plant matches the type of *R. decurrens* Mitt., though the type plants of this species are exceptionally robust. The sister relationship between *R. decurrens* and remaining four morphological entities in clade B were fully supported. These four entities are described below.

The next morphological entity within clade B comprised two individuals from Vanuatu in a fully supported monophylum (PP = 1.0), and three individuals from Nabukelevu mountain on Kadavu Island, Fiji in another fully supported monophylum (PP = 1.0). These individuals strongly resemble *R. sp.* NSW895234 in their contiguous leaf-lobes and relatively small lobules, but are pinnately branched, and the lobules on primary shoots have a more ampliate interior margin that may exceed the opposing stem margin. Differences in female bract morphology are apparent between sampled individuals, in the present species (*R. sp.* NSW974478) the bract lobes are closely overlapping (Figs 36, 37), whereas in *R. sp.* NSW895234 they are divergent and spreading. These differences may or may not be consistent. Both individuals in this clade were pendulous from trees overhanging a stream at about 800 m asl. Three individuals from Nabukelevu mountain on the Island of Kadavu in Fiji form a fully supported monophylum nested within the remaining individuals. These individuals are the same morphological entity as Vanuatu individuals, and all are referred to as *R. sp.* NSW974478.

The relationships of these two clades to each other and remaining individuals were unresolved. The remaining eleven individuals comprised two morphological entities. One was represented by 9 individuals from the Wet Tropics of north-east Queensland. This morphological entity is characterised by the ruminant ornamentation on the leaf-lobe cell surfaces. This feature is unique, not only within subg. *Radula* but also within the genus. The lobules are rhombiform with an ampliate interior margin exceeding the opposite stem margin, and none of the margins are reflexed (Figs 5–7). This form corresponds to no type material, and is described below as *R. oreopsis* M.A.M.Renner.

The other form was represented by two individuals from Borneo and Vanuatu. This plant bears punctulate-undulate ornamentation. While similar in lobule size and shape the exterior lobule margin has a tendency to be shallowly undulate as it is addressed toward the leaf lobe (Figs 31, 32). The two individuals were collected as epiphytes. They were nested within *R. oreopsis* without support, and did not group together in the phylogeny though relationships within their clade were largely unsupported.

Discussion

What is *Radula javanica*?

The molecular phylogeny unites a morphologically heterogeneous array of individuals from across Australasia and the Pacific into a single fully supported clade. Unfortunately, no supported monophyla, corresponding to any groups defined by morphological or ecological data were resolved within this clade. Individuals variously possess character states thought to be diagnostic of *R. erigens*, *R. longispica* and *R. reflexa* in addition to *R. javanica*, according to the current circumscription of these species in this region (So 2006, Renner et al. 2013b). Variation in ecology and morphology appear correlated to some degree. Individuals with reflexed lobule apices, and near complete fragmentation of leaf-lobes on mature shoot sectors (Fig. 8) were collected on rocks and logs within waterways, at low altitudes (generally less than 300 m) in Australia and Fiji. These individuals have the same morphology as those Australian and Fijian individuals previously determined as *R. reflexa*. Individuals with quadrate-oblong lobules having reflexed lobule apices and interior lobule margins, and infrequent caducous leaf production (Fig. 11) were collected on rocks in and around waterways in Australia. These individuals have the same morphology as those Australian individuals previously determined as *R. multiflora*. Individuals with large quadrate lobules having an ampliate interior margin and infrequent production of caducous leaf-lobes (Fig. 14) were collected as epiphytes at mid altitude (around 500 metres) within tropical rainforest on Rarotonga. These individuals correspond with the type of *R. cordiloba*. Prior to the molecular analysis, I was prepared to accept three separate species as occurring in Australia on the basis of morphological and ecological evidence, despite morphological continuity and overlap (see Renner et al. 2013d). The molecular evidence gathered in this study is equivocal with regards to that interpretation.

There are several explanations for the lack of congruence between morphological and molecular groups. At one extreme, incomplete lineage sorting between species of relatively recent origin could explain incongruence

between the chloroplast gene tree and the actual species tree. In this case morphotypes correspond to non-monophyletic semi-cryptic species. An alternative explanation is that *R. javanica* comprises a wide-ranging species whose populations remain connected via dispersal and colonisation. Colonisation could be frequent enough to unify all individuals into what is effectively a single population that exhibits considerable phenotypic plasticity, or polymorphism, perhaps generated in some parts of its distribution and then dispersed to others. Some intermediate scenario, involving dispersal events between habitat islands occurring on similar timescales to divergence events within habitat islands may facilitate the generation and maintenance of polymorphism within the metapopulation that exists across the Pacific. Divergence events driven by both selection and drift could underly the generation of novel morphotypes, and this generation could be balanced by dispersal between habitats prior the acquisition of reproductive isolation. This could explain the co-occurrence of morphologically different but ecologically similar individuals, as with the *R. reflexa* and *R. multiflora* morphs of *R. javanica* in Australia. However, this study's sampling of individuals is limited in geographic extent and the molecular markers used are indicative of chloroplast lineage only, and while relatively fast evolving, may not mutate fast enough to detect very recent divergence events. Molecular markers sensitive to patterns of interbreeding, e.g. SSR's (Ramaiya et al. 2010) could be used to further investigate mechanisms underlying the origin and maintenance of morphological variation within what appears to be a single species. Greater specific diversity may yet be resolved within the broad circumscription of *R. javanica* accepted here.

Molecular data provides some support for the current view that *Radula javanica* is a morphologically variable, ecologically tolerant, geographically widespread species. Individuals corresponding to the type of *R. oecania*, and several undetermined (possibly undescribed) morphological entities, are not members of the *Radula javanica* clade even though they are currently regarded as synonyms, or would be attributed to *R. javanica* given its current circumscription. Although individuals of *R. oecania* have several distinctive morphological features, individuals in other clades exhibit only subtle differences in size and shape of leaf-lobes and lobules from *R. javanica*. In addition to polymorphism within *R. javanica*, subtly differentiated reproductively isolated lineages representing semi-cryptic species may be present throughout the Pacific. Both factors complicate morphological species circumscription and identification.

'Topotype' material of *R. reflexa* and *R. multiflora* was lacking from this study. There were no individuals included in this study that were comparable with the types of these two species (*R. multiflora*: G00282365!; *R. reflexa*: BM! G00046053!). The descriptions and fragmentary types appear to have more to do with each other than with anything in Australasia and the Pacific. Given the lack of correspondence with type material these species may not be present in sampled regions, and are doubtful synonyms of *R. javanica*, but more conclusive investigation is required to clarify this.

Far from being diagnosable by single distinctive morphological characters such as the presence or absence of caducous leaf-lobes, the presence of reflexed lobule margins, or whether the lobule apex is turned outward from the stem, species within *Radula* subg. *Radula* may only be separated by subtle differences in leaf-lobe and lobule size, shape and orientation. Differences of this nature and degree are not only difficult to describe, they are virtually impossible to apprehend independent of molecular data corroborating their significance. The species with which these entities must be compared (*R. javanica*) is itself polymorphic across a broad geographic range, which compounds these difficulties to the point of intractability.

Nowhere is this intractability better illustrated than by comparing *R. sp.* NSW974478 (Figs 29, 30) and *R. sp.* NSW895234 (Figs 35, 36). These two entities are morphologically distinct from other sampled species in *Radula* subg. *Radula* by their contiguous leaf lobes, widely spaced secondary branches, and rhombiform lobules whose apex is turned slightly outward away from the stem apex. The two species are indistinguishable with the exception of branching pattern, which is pinnate in the former and almost pseudodichotomous in the latter; and the lobule whose ampliation on the interior margin is slightly more pronounced on primary shoots in the former. Although known from a handful of collections each, the two species share similar ecology, both form pendulous wefts that hang from branches and trunks over waterways in mid elevation tropical rainforest. Incredibly, the geographic ranges of both overlap – while the former was collected in Vanuatu only, the latter was collected in Vanuatu and Fiji. Hence, these two morphologically similar, ecologically equivalent, sympatric but reproductively isolated and relatively unrelated species may co-occur on Vanuatu and elsewhere in the Pacific. Whether their morphological similarity is due to convergence under selection, drift through morphospace, or some other process is not known. Presumably both species share a derived morphology, but even this remains untested.

Another character state almost certainly derived within *Radula* subg. *Radula* is the ruminant ornamentation present on the surface of leaf-lobe cells in *R. oreopsis*. This feature is unique to *R. oreopsis* among sampled species. The geographic restriction of ruminant surface ornamentation to individuals from the Wet Tropics of Queensland, and the presence of other more subtle morphological differences between individuals from

the Wet Tropics of Queensland and close relatives from overseas builds a strong case for recognition of *R. oreopsis* despite the fact that it is rendered paraphyletic (sensu Nelson 1971) by individuals from Borneo, Vanuatu, and Fiji. These comprise two morphological entities, one individual of which is nested among *R. oreopsis* individuals with support, the other relationships are unsupported. Weak phylogenetic signal may explain the lack of support, sequence evolution may be slow relative to speciation rate (Funk & Omland 2003). The three chloroplast markers may not have evolved rapidly enough to diagnose monophyletic groups, and both *R. oreopsis* and *R. sp. NSW974485* may be found monophyletic by more sensitive markers. The fact that *R. oreopsis* can be diagnosed by a unique kind of leaf-lobe cell surface ornamentation argues strongly for its monophyly within the context of current sampling. However, only a small fraction of Melanesia and Oceania was included in this study, both in terms of geographic and specific coverage. More extensive sampling may identify other species sharing this character, which may or may not be close relatives of *R. oreopsis*. The unique cell ornamentation in *R. oreopsis*, but not in close allies hints at rapid morphological evolution. The only time-calibrated study of morphological evolution within liverworts, in *Leptoscyphus*, measured transformation rates in millions of years (Devos & Vanderpoorten 2008).

Speciation and diversification in Pacific Radula

The Pacific is basically one enormous dispersed archipelago, a multitude of isolated habitat patches. The dispersed nature of land within island archipelagos means spatial isolation could contribute to origin and maintenance of species diversity across the Pacific. Most of the habitat patches (for both marine and terrestrial habitats) were formed by volcanic activity (Nunn 1998), and dispersal and colonization have contributed to the biota of many Pacific Islands. Dispersability may be a key factor determining species range and connectivity among populations across the Pacific. In reef fish, another organism group occupying dispersed and often isolated habitat patches across the Indo-Pacific, some species show higher levels of connectivity among populations than others (Horne et al. 2008). Pelagic larval duration influences population connectivity, and species with longer pelagic larval duration typically exhibit higher levels of gene flow and connectivity between populations (Bowen et al. 2013). In reef fish with short pelagic larval durations genetic isolation of peripheral populations is known (van der Meer et al. 2013).

Rather than disperse by a water-borne larval stage, bryophytes disperse by air-borne spores and the durability of these spores may have similar consequences in bryophytes as pelagic larval duration in reef fish. In *Radula*, as in all liverworts, differences in spore durability between species was demonstrated by van Zanten & Gradstein (1988). Spore durability must influence the capacity of species to firstly disperse to isolated habitats and secondly remain in genetic contact with parental populations. Many or all the habitat islands across the Pacific may be effectively isolated by low spore durability, and what constitutes an isolated habitat patch at the periphery of a species distribution may vary between species in relation to their spore durability. Effectively isolated habitats may exist in the middle of a species distribution.

The isolation of peripheral populations may promote divergence (Mayr 1942). Newly isolated populations possess a subset of alleles from the parental population and if the peripherally isolated population is initially small and local, under drift alleles will be lost from this population at a faster rate than in the parental population. Divergence occurs as allele frequencies change, and novel characteristics may become fixed rapidly particularly when population size is small (Vanderpoorten & Long 2006).

Divergence through isolation of peripheral populations may be mediated by drift or selection. Ecological factors may operate within islands to drive divergence between subpopulations of colonists. Two species of *Howea* palm on Lord Howe Island are thought to have diverged in sympatry (Savolainen et al. 2006). Alternative explanations involving earlier allopatric isolation of diverging populations on a younger, larger Lord Howe Island have been proposed (Stuessy 2006), but even this scenario does not posit an island large enough relative to the spatial scale of wind pollination and bird dispersal in the species involved for effective isolation (Savolainen et al. 2006). The processes leading to divergence (rather than the spatial arrangement of the products of a divergence event) can be divided into active and passive or neutral processes, where natural selection is an active process, and drift is a neutral process. Under selection reproductive isolation may be acquired in very short timeframe, and the rapid acquisition of reproductive isolation due to selection has been demonstrated in salmon, where significant partial reproductive isolation between river- and lake-spawning populations in sympatry was acquired in 13 generations (Hendry et al. 2000). Selection mediated divergence despite ongoing gene flow between populations has been documented in *Mimulus* (Macnair & Gardner 1998).

Founder flush speciation describes a scenario wherein novel material upon which selection could act is generated in colonizer populations by recombination as a result of population expansion from a small pool of founding individuals (Templeton 2008), and this may contribute to diversification on newly colonized islands.

Embedded daughter species can render parental species paraphyletic, and asymmetrically paraphyletic relationships will persist until sorting renders parental species monophyletic (Funk & Omland 2003). If dispersal and diversification events occur at rates equivalent to the rate at which species sort to reciprocal monophyly, and both are ongoing in space and time a paraphyly disequilibrium may be maintained as the normal pattern of phylogenetic relationships between species. This paraphyly disequilibrium would result from the dynamics of dispersal and colonization, divergence, and lineage sorting within the context of an extended archipelago of isolated habitat patches. This may actually be the case in *R. javanica*, in which case the gene tree may bear little relevance to evolutionary entities. It seems to be the case in *R. oreopsis* and its near relatives, where *Radula oreopsis* appears to be a neo-endemic species, isolated either by contraction of tropical habitats in northern Australia during dryer glacial periods (Kershaw et al. 2007) or by dispersal. Alternatively the species does occur elsewhere, probably Papua New Guinea, but has not been detected.

If mode and tempo of speciation across the Pacific differs from that in Melanesia, different patterns of relationship between species should be apparent. Melanesian sister species might be older, and therefore reciprocally monophyletic. If Melanesia exports species to the Pacific, species from the latter should be nested within lineages dominated by Melanesian species. If the Pacific also exports diversity back into Melanesia more complicated patterns should manifest in gene trees. If the prevalence of reciprocally monophyletic relationships between species declines westward across the Pacific, phylogenetic diversity may appear to exhibit a decline, and Pacific Islands may appear to be evolutionary graveyards from a purely phylogenetic perspective.

The first step would be a broad survey targeting one or more groups to establish whether patterns of relationship between species change in different parts of the Indo-Pacific region.

Taxonomic implications

Within *Radula* subg. *Radula* across the Pacific, broad species hypotheses have been inferred inappropriately. The underestimation of lineage diversity by morphologically based species circumscriptions is now a common theme in bryophyte systematics (Shaw 2001; Heinrichs et al. 2009, 2010, 2011; Vanderpoorten & Shaw 2010). This may be due to the species being defined on the basis of gross, often qualitative and often single, morphological characters. The lines of strict morphological discontinuity separating species simply do not exist at the level of inquiry applied by recent studies. Many subtle yet consistent differences in size and shape, and micromorphological and anatomical characters that potentially inform species circumscription have been overlooked. This is becoming a theme in bryophyte phylogenetic systematic studies where morphological species diversity often increases in lieu of molecular data (Renner et al. 2011; Medina et al. 2012; Renner et al. 2013a)

Reports of some species for the Pacific and Australasian region having types elsewhere may be in error. No individuals exhibiting correspondence with the types of *R. multiflora* or *R. reflexa* were sampled by this study.

Inherent challenges for morphological species circumscription were manifest in this study. Morphological variation and polymorphism at the population level can mean that while differences are apparent between individuals from the same geographic region, molecular data suggests these are members of the same morphologically variable species, as seems the case with *R. javanica*. In contrast, apparently convergent evolution in different lineages means that individuals that share morphological form may not be nearest relatives, as appears the case in *R. sp.* NSW974478 and *R. sp.* NSW895234; and also in *R. oecania* and its apparently distinct morphological mimic *R. sp.* NSW974317.

The fact that *Radula* species often exhibit dimorphism in their shoot systems (Renner et al. 2013c) has not been explicitly acknowledged in previous studies. Failure to recognize this contribution to intra-individual variation may have enhanced the impression of morphological continuity between different species, as lobules on primary and secondary shoots can be quite different within individuals, and lobules on secondary shoots of individuals belonging to different species can appear more or less similar.

Extraneous challenges for morphological species circumscription also manifest in this study group. Type material is often fragmentary, as in *R. multiflora* and *R. reflexa* for example. Often type specimens consist of secondary shoots only, which typically exhibit different morphology from primary shoots in pinnately branched plants (Renner et al. 2013c), and may not bear characteristics diagnostic of the species. Often types are not representative of the morphology of individuals belonging to species they are supposed to represent.

The protologue and diagnosis of many species described in the 19th and early 20th centuries describe gross morphological characters in general terms. Shape differences that might be present in type material, and diagnostic of species are generally poorly quantified. Many protologues apply more or less equally well to more than one entity.

Not including collections from type localities in the phylogeny hinders applications of names to entities.

Next steps

The best approach to reconciling observed patterns of variation with species and resolving names may be local. Having the opportunity to at least subjectively synthesise ecological data with morphological data, particularly patterns of morphological data, may facilitate the resolution of entities within a region as ecology provides another source of character data upon which individuals can be grouped, and bryophyte species are often well-defined ecologically (Shaw 1985). Local species resolved on the basis of morphological and ecological data could be targeted for confirmation and comparison with those from other areas by broader scale studies. Workers might provide informal names to entities in their regions, as this study has done, to avoid increasing whatever synonymy burden already exists. However, the re-collection of material from type localities will be crucial in future attempts to relate entities to names. The broad scale yet fragmentary snapshot captured by this study is insufficiently fine-grained to yield conclusive insight into the full complexity of relationships and diversity across the Pacific. On the other hand, it does indicate the existence of that complexity.

Taxonomic Treatment

Key to species of *Radula* subg. *Radula* in Australasia

The first character presented is usually diagnostic. Other characters are included to: 1) facilitate identification as far as possible, 2) identify couplet selection errors at subsequent steps of the key, and 3) aid in the identification of species that are not included in this treatment, either because they are novel, or unrelated. Comparison of shape characters must be made on the basis of hydrated, slide-mounted material.

This key does not include Pacific and Melanesian species because the author remains largely ignorant of them and any attempt at their inclusion would prove both inadequate and incomplete, and possibly misleading.

- 1 Marginal gemmae (always present) irregular discoidal to sub-rugose, abundant from leaf-lobe margin. Caducous leaves absent. Living plants clear yellow-green. Shoot systems not obviously dimorphic (subdimorphic in some robust individuals growing on the bark of *R. grandis*), typically irregularly branched, shoot system generally tightly adherent to substrate. Leaf-lobe cell surfaces smooth 2
1. Marginal gemmae absent. Caducous leaves rare to abundant on mature shoot sectors (evidence of caducous leaves takes the form of leaves whose leaf-lobe has dislocated, with the line of dislocation being comparable across different leaves whose lobe is missing). Living plants mid- to brown-green or milky yellow-green. Shoot systems typically dimorphic, pinnately branched (except *R. madagascariensis* which has monomorphic irregular shoot systems) and generally free of substrate to some degree. Leaf-lobe cell surfaces rugose or ruminant (except *Radula* sp. Moa Island CANB9500187 which has smooth leaf-lobe cell surfaces) 3
- 2 Lobules on primary shoots with obtuse to acute apices, sometimes drawn out into an acuminate tip; interior margin ampliate but not overlapping with adjacent lobules. Leaf-lobes plane, shoots complanate *Radula acutiloba*
2. Lobules on primary shoots with rounded to obtuse apices, never drawn out into an acuminate tip; interior margin ampliate and occasionally overlapping with adjacent lobules. Leaf-lobes concave with inrolled exterior margin, shoots flattened-cylindrical *Radula grandis*
- 3 Leaf-lobe cell surfaces smooth *Radula* sp. Moa Island (CANB9500187)*
3. Leaf-lobe cell surfaces ornamented 4
- 4 Leaf-lobe cell surface ruminant. Lobules flat, broadly triangular *Radula oreopsis*
4. Leaf-lobe cell surface punctulate to verrucose. Lobules flat or with reflexed margins or apex, rectangular to quadrate or rhombiform 5
- 5 Shoot systems monomorphic, irregularly branched, primary shoots relatively small up to 1 mm wide. Leaf-lobe cell surfaces verrucose with dense and heavy ornamentation. Lobules rectangular *Radula madagascariensis*
5. Shoot systems dimorphic, pinnately branched, primary shoots relatively large up to 2 mm wide. Leaf-lobe cell surfaces punctulate or rugose with ornamentation 6
- 6 Lobules quadrate, interior margin on primary shoots ampliate, exterior margin parallel with stem, antical margin more or less perpendicular to stem, flat *Radula mittenii*
6. Lobules rhombic, interior margin on primary shoots ampliate or not, exterior margin inclined away from stem, antical margin inclined toward stem, usually with apex or margins reflexed to some degree..... *Radula javanica*

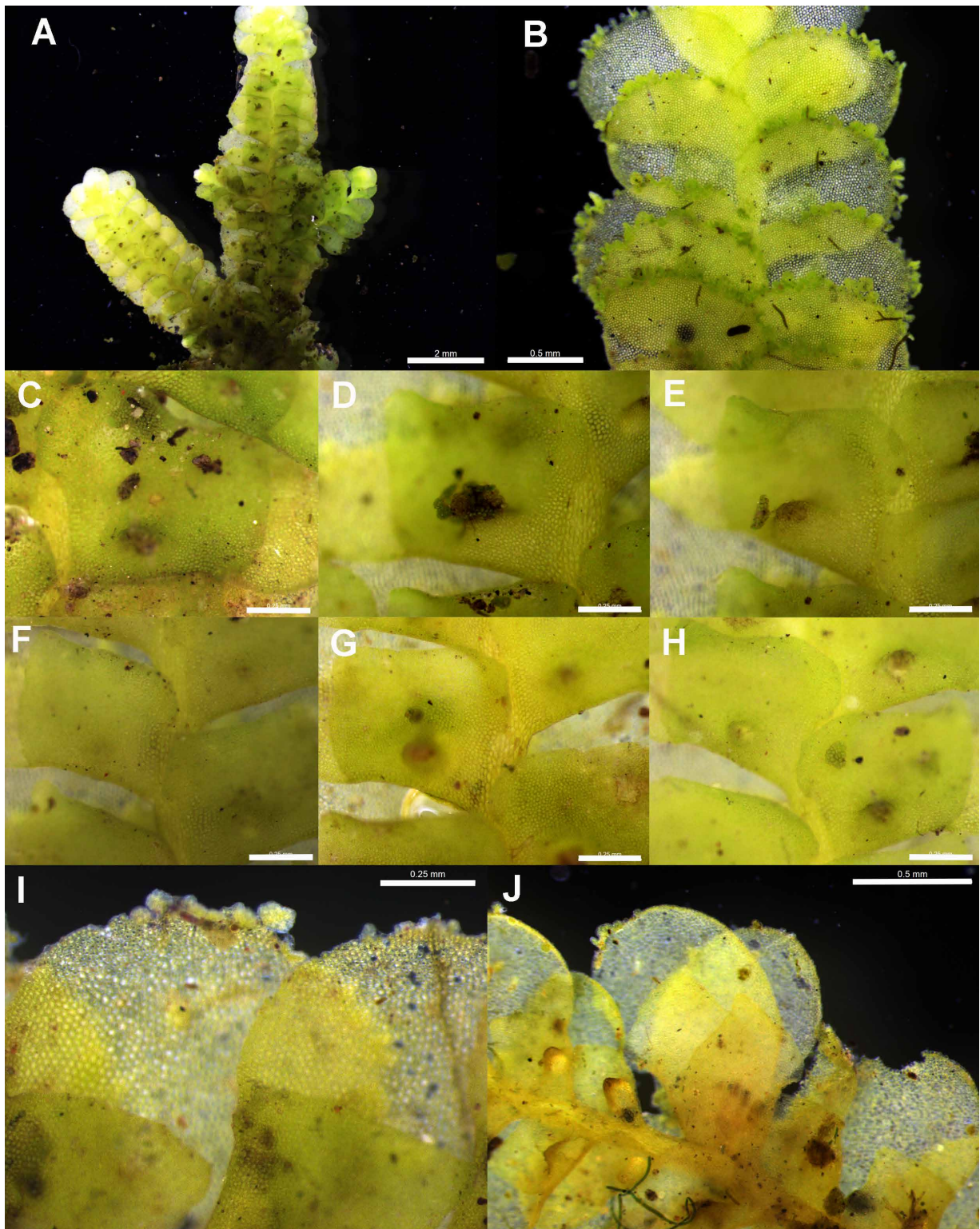


Fig. 2. *Radula acutiloba* Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μ m). C-E: Primary shoot lobules (250 μ m). F-H: Secondary shoot lobules (250 μ m). I: Secondary shoot lobe margins (250 μ m). J: Female bracts (500 μ m). All from NSW976176.

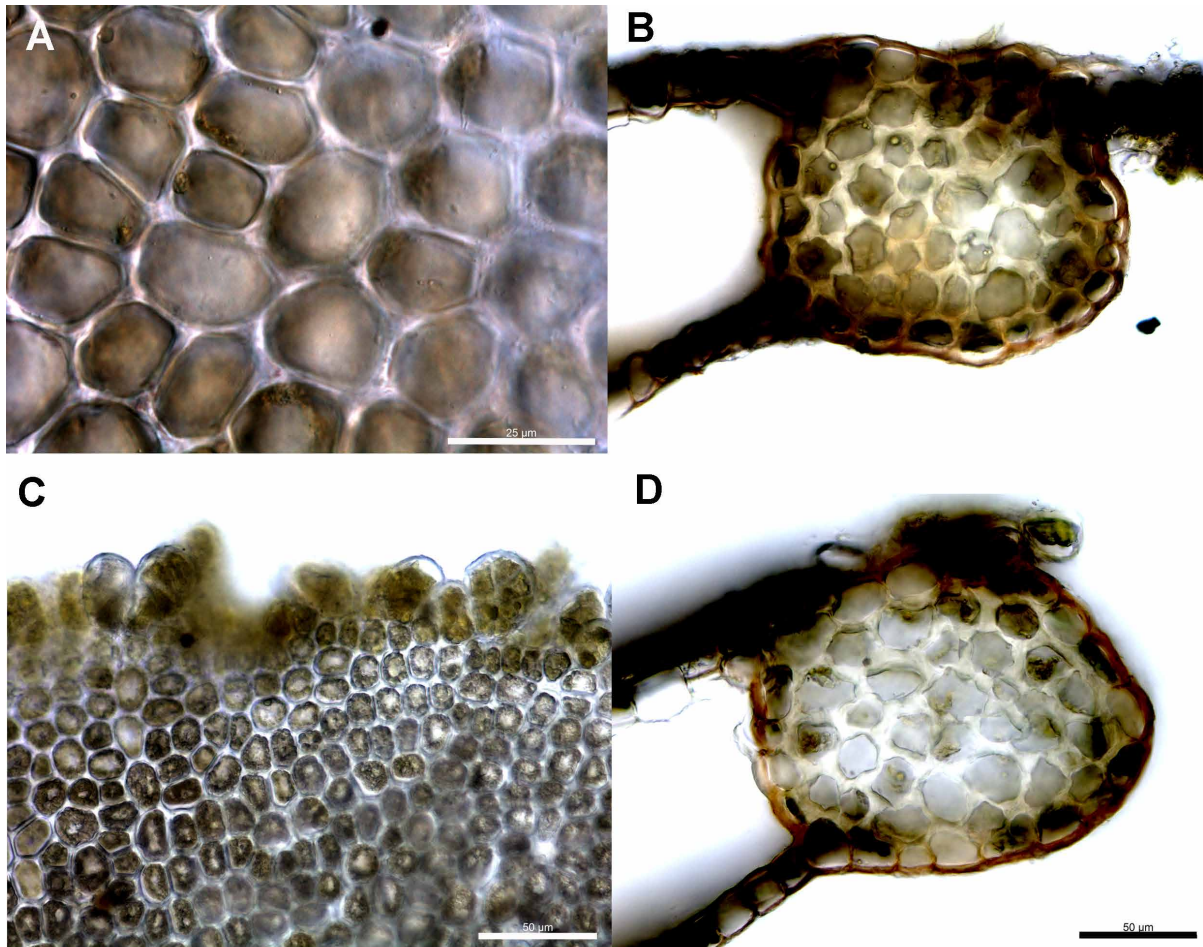


Fig. 3. *Radula acutiloba* Plate B. A: Leaf-lobe medial cell surface, showing lack of ornamentation (25 μm). B, D: Transverse sections of primary stems (50 μm). C: Leaf-lobe margin (50 μm). All from NSW976176.

The absence of leaf-lobe cell surface ornamentation in this large, pinnately branched plant with dimorphic shoot systems is inconsistent with other members of the *Radula* subg. *Radula* crown clade, and may indicate that this species belongs in *R.* subg. *Volutoradula*. However, this is conjecture and the species is included here because no other regional species of *Radula* subg. *Volutoradula* are known, and it is phenetically similar to species of *Radula* subg. *Radula*. Unfortunately, molecular data was not extracted from this specimen

Radula acutiloba Steph. *Hedwigia* 28: 271. 1889

Type: Australia, Queensland, *F. M. Bailey* 37, herb. Brotherus. (FH!, G-14976!).

Radula papulosa Steph. *Journal of the Linnean Society, Botany* 29: 272. 1892

Type: “wood beyond Chinese”, Dannevirke, Hawkes Bay, *Colenso a.1643*, (lectotype, designated by Castle 1967: G-22376!; isolectotype: BM000661176!, WELT-H007728!).

Description [from CANB8002399]: Forming loosely interwoven patches of shoots, yellow-green when fresh fading to pale yellow brown in herbarium. Shoot systems irregularly pinnately branched. Shoot systems dimorphic, 1.3–1.8 mm wide and up to 40 mm long, branches smaller in stature than parent shoot, typically remaining small stature, occasionally attaining similar stature to parent shoot. Older shoot sectors retaining leaf-lobes. Stems 110–180 μm diameter, with cortical cells in a single tier of 17–25 rows. Cortical cell walls faintly yellow- to brown-pigmented, variable within individuals, typically darker in older shoot sectors, external free cortical cell wall continuously and evenly thickened, radial longitudinal cortical walls thin or continuously thickened, with or without triangular to bulging trigones; medullary cells in 20–28 rows; walls unpigmented to brown-pigmented, variable within populations and even within individual stem, variably thickened, from triangular trigones at angles and thin walls between, to large bulging trigones that are

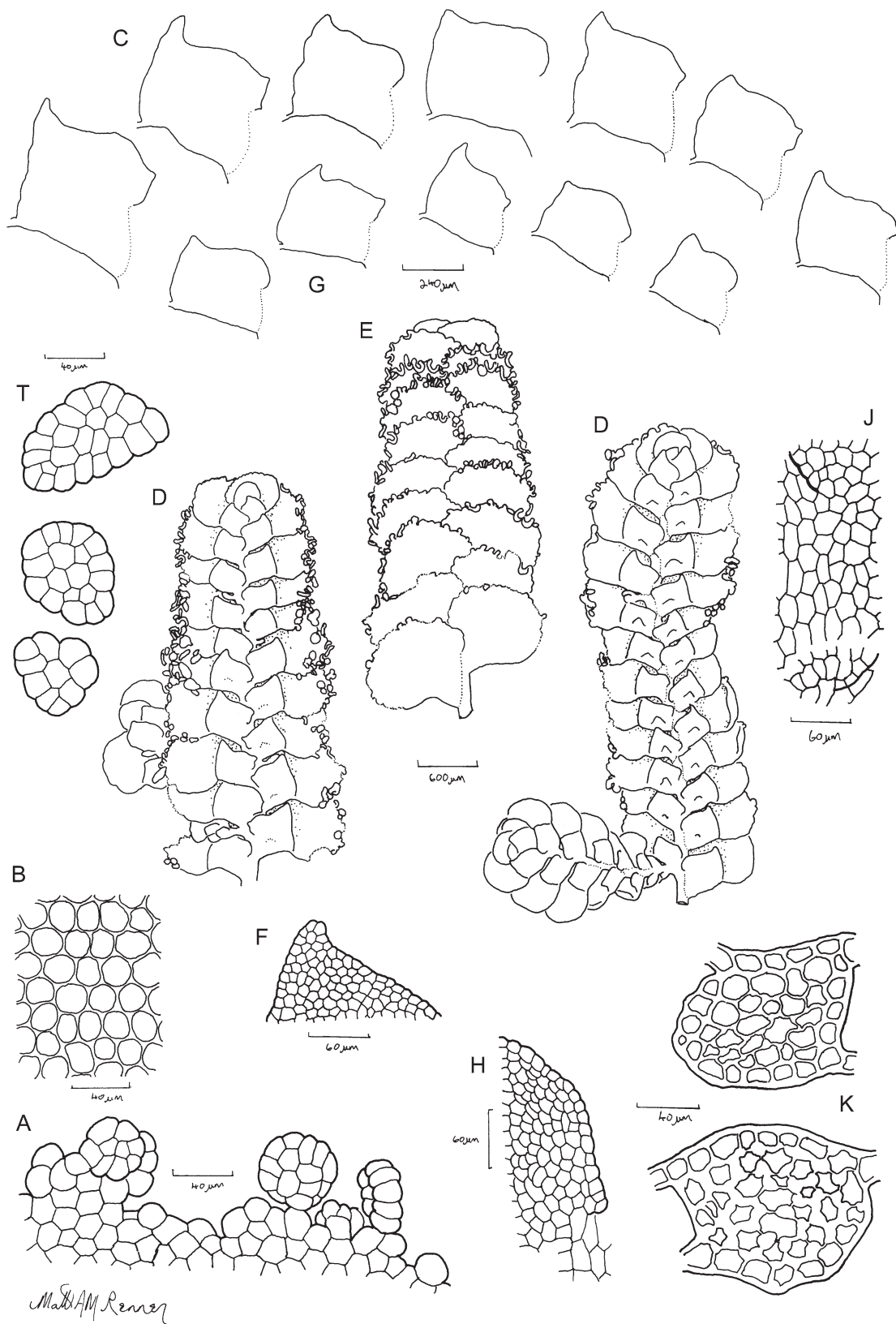


Fig. 4. *Radula acutiloba* Line drawings. A: Lobe marginal cells showing gemmae. B: Lobe medial cells. C: Seven lobules from primary shoots. D: Ventral view of primary shoot. E: Dorsal view of primary shoot. F: Lobule apex. G: Five lobules from secondary branches. H: Lobule interior margin. J: Cells on dorsal stem surface. K: Transverse stem sections. T: Gemmae. All from NSW896401

frequently confluent across medial walls (variable within populations), inner tangential walls continuously thickened, with or without triangular to bulging trigones. Cortical cells on dorsal stem surface arranged in straight longitudinal rows on young and mature shoot sectors. Leaf-lobe exceeding dorsal stem mid-line, overlapping across at least one dorsal cortical cell row, dorsal leaf-free strip absent. Leaf insertion attaining the ventral stem mid-line or not, leaving zero or one ventral cortical cell rows leaf-free, ventral leaf free strip variably present or absent. Leaf lobes rotund 680–1200 μm long by 650–1100 μm wide, imbricate, not falcate, acroscopic base not sharply deflexed away from stem, flat to weakly concave, interlocking over the dorsal stem surface, stem not visible between leaf lobes in dorsal view; margins irregularly repand and undulate due to proliferation of marginal cells, particularly in the youngest mature leaves, becoming erose in older mature leaves as gemmae fragment from margin, the interior lobe margin ampliate, usually attaining the opposite stem margin, all margins curved; angle between postical lobe margin and keel 150–180°. Lobules quadrate to short rectangular, remote to contiguous, one quarter the lobe area, 380–820 μm long by 290–540 μm wide, keel straight to scarcely curved or arched, angle between keel and stem 100–120°, keel turning through 30° at keel-lobe junction, keel apex and postical lobe margin flush; interior lobule margin free for one third its length, free portion ampliate, frequently attaining the opposite stem margin and concealing the stem in ventral view, occasionally with a triangular tooth on the interior lobule margin; acroscopic margin straight to arched, apical portion inclined inward toward the stem; apex acute to acuminate, free exterior margin straight to shallowly curved, margins more or less entire. Lobe-lobule junction postical to the acroscopic end of stem insertion. Attached to stem along two-thirds of the interior margin, stem insertion arched, gently curved at acroscopic and basicopic ends, not revolute. Lobule apex bearing a single papilla, with another papilla situated on the interior lobule margin above the stem insertion, typically at the apex of an indistinct projection or distinct triangular tooth. Leaf lobe cells rounded, arranged in loose rows, uniformly sized, 15–20 μm long and wide, thin walled with concave trigones, medial wall thickenings absent. Cells of lobe margin similar in size to those of middle, rounded, interior and exterior cell walls not differentially thickened, but marginal cells bulging, and proliferating as described above. Leaf lobe cell surface smooth. Oil-bodies one per cell, brown, coarsely rugose, ovoidal. Asexual reproduction by subdiscoïd gemmae produced from lobe margins, gemmae unistratose, variably sized and shaped, with 9–30 cells, when exceptionally large appearing subthalloïd. Dioïcous (?), sexual organs not seen.

Figs 2–4

Distribution and ecology: Australia, New Zealand and Papua New Guinea. In Australia *Radula acutiloba* is currently known from several widely separated sites on the central and south-eastern coast, between latitudes 24°–38° S. *Radula acutiloba* inhabits tropical dry rainforest and scrubs, and wet sclerophyll forests. It is lithophytic on rocks or epiphytic on tree trunks and branches amongst mosses, lichens and other hepatics. It is known to colonise exotic ornamental trees in semi-urban settings, as Mt Wilson in the Blue Mountains (New South Wales, Australia). In an unusual situation *R. acutiloba* grew on cliff face above the beach at East Boyd Bay in south-eastern New South Wales.

In Papua New Guinea *R. acutiloba* has been collected as an epiphyte in montane rainforest at around 1500 m asl.

Identification: *Radula acutiloba* is a distinctive species that is only likely to be confused with a few related species that share with it the yellow-green colour and marginal subdiscoïd gemmae. It is the only species currently known in Australia with this combination of characters.

The production of subdiscoïd gemmae in dense proliferating masses from the leaf-lobe margin is diagnostic of *Radula acutiloba* in Australia. In some cases the leaf lobe marginal cells divide so vigorously that the lobe margin becomes undulate due to the increase in marginal length introduced by the dividing cells. Gemmae production is initiated on the youngest leaves, and the density and size of gemmae on the leaf lobe margins increases rapidly as the leaves age. The majority of gemmae have matured by the fourth pair of leaves from the shoot apex. Behind this leaf pair the rate of dissemination must be greater than the rate of production, because the density of gemmae on the leaf lobe margin decreases rapidly, leaving the leaf lobe margins on old shoot sectors erose, and in some cases torn and fragmented, with few or no gemmae attached to the margins. No gemmae are produced from the ventral leaf lobe surfaces.

In New Zealand another species of subg. *Radula*, *R. grandis* Steph., produces subdiscoïd gemma. However, the gemmae of *R. grandis* are not produced in the same abundance as in *R. acutiloba*, and I have never observed the leaf-lobe margin undulating in order to accommodate the proliferating marginal lobe cells. Using these differences to arrive at a determination is probably best on the basis of experience. Better characters can be found in the shape and spacing of lobules. The lobule apex of *R. acutiloba* is obtuse to acute, whereas in *R. grandis* the lobule apex is rounded. The interior lobule margin is often angular, sometimes with a distinct point on the ampliate portion, while in *R. grandis* the interior lobule margin is rounded. On primary shoots

the lobules of *R. acutiloba* are contiguous to slightly imbricate and do not overlap the stem completely, whereas in *R. grandis* the lobules are densely imbricate and overlap the ventral stem surface completely.

Radula acutiloba is similar to several other gemmae-producing species belonging to subg. *Radula*, including the generitype *R. complanata*. While *R. complanata* is readily identified by its monoicy, other species such as *R. constricta* may be more difficult to distinguish. One specimen of *R. constricta* examined had distinctly crenulate leaf-lobe margins and bulging leaf-lobe cells, however whether this is consistent within Asian populations of the species, and therefore represents a fixed morphological difference between these species is not known. Currently the most robust character upon which determination can be based is provenance. *Radula acutiloba* is the only member of gemmae-producing subg. *Radula* species currently known from Papua New Guinea and Australia, while in New Zealand its distribution overlaps with *R. grandis*, as noted above.

Variation: Within individuals increasing lobule size is associated with sharper apices and more pronounced angular projection on the interior lobule margin. Lobule size is correlated with shoot stature, which can differ within and between individuals. Larger shoots possess leaves with large lobules and these tend to have acute apices and pronounced angular interior margins. Individuals from Papua New Guinea tend to have reflexed antical lobule margins.

Remarks: The relationships between *R. acutiloba* and extraterritorial species require investigation in a global context. The species is morphologically similar to all other members of its clade, however is distinguishable from some on the basis of micromorphological characters. Some Chinese specimens of *R. constricta* have distinctly bulging leaf-lobe cells, and a crenulate leaf-lobe margin, features not observed in Australasian specimens, that may support the maintenance of separate species status.

Nomenclature: *Radula papulosa* was synonymised with *R. acutiloba* by Yamada (1987). This was followed by So (2005) but not by Renner (2005) or Meagher and Fuhrer (2003).

Specimens examined: PAPUA NEW GUINEA: WESTERN HIGHLANDS: Kagamuga, 10 km E of Mt Hagen, 5° 51' S 144° 19' E, 1580 m, 22 Jun 1982, *H. Streimann 20462* (CANB8212405); *H. Streimann 20464* (CANB8212407); EASTERN HIGHLANDS: Lapegu, 6 km SW of Goroka, 6°06'S 145°20'E, 1520 m, 11 Apr 1982, *H. Streimann 18410* (CANB8204190).

AUSTRALIA: QUEENSLAND: BURNETT: Hurdle Gully, 14 km WSW of Monto, 24° 54' S 149° 58' E, 300 m, 16 Jan 1980, *H. Streimann 9871* (CANB8002399); *H. Streimann 9873* (CANB8002401); *H. Streimann 9880* (CANB8002408); NEW SOUTH WALES: NORTHERN TABLELANDS: Oxley Wild Rivers National Park, Chandler River, 100 m downstream of track from Checks Lookout, 30°32'30"S 152°01'26"E, 540 m, 1 Jan 2012, *M.A.M. Renner 5889* (NSW976716); Hillgrove Gorge [near Armidale], 30°33'35"S 151°53'17"E, 2 Nov 1903, *W.W. Watts 754* (NSW764131); Hillgrove Gorge, 30° 34'S 151°54'E, Nov 1903, *W.W. Watts 754* (NSW764131); CENTRAL TABLELANDS: Mount Wilson, roadside trees, just above Zig-Zag, 33°30'S 150° 23'E, 18 Jun 1983, *W.B. Schofield 79482*, *H.P. Ramsay & M.I. Schofield* (NSW379103); Mount Wilson, 23 km NNE of Katoomba, 33° 31' S 150° 21'E, 980 m, 1 Nov 1984, *H. Streimann 31539* (CANB734323); CENTRAL COAST: Blue Mountains National Park, Coxs River, Breakfast Creek, Carlon Creek south of Ironpot Ridge and Green Gully, 33° 47' 53" S 150° 13' 19" E, 400 m, 8 Jan 2012, *M.A.M. Renner 5890 & J. Bevan*, (NSW978099); SOUTH COAST: East Boyd Bay, 5 km S of Eden, 37° 7'S 149° 54' E, 2 m, 25 Mar 1977, *H. Streimann 4542* (CANB7706914).

NEW ZEALAND: NORTH ISLAND: Alton, Wairoa, June 1935, *E.A. Hodgson* (CHR-H4341, FH00284640); 'from Glenroys', *W. Colenso a.1450* (BM000661175); Wellington District, Southern Hawke Bay, Waipukurau, A'Deane Bush Scenic Reserve, 39° 55' 57" S 176° 17' 59" E, 290 m, 21 Feb 2012, *M.A.M. Renner 6262* (NSW896401); Wellington District, Ahi Paku Station 30 km east of Tauherenikau, Whakarua Road, Tawhiriwaimanuka Stream, 42°21'S 175°25'E, 26 Nov 2001, *V Stajsic 3171* (MEL2181419).

Radula oreopsis M.A.M. Renner sp. nov.

Type: Australia, Queensland, Cook, Daintree National Park, Mossman Gorge, Rex Creek, upstream from swingbridge, 16° 28' 13" S 145° 19' 42" E, 105 m, 24 Mar 2012, *M.A.M. Renner 6270*, *V.C. Linis & E.A. Brown* (holotype: NSW896415, isotypes: BRI, F).

Diagnosis: Distinctive in the ruminant ornamentation of the leaf lobe cell surfaces, a feature unique among Australasian species and possibly the genus; the asymmetrically rhomboid lobules imbricate on primary shoots and obscuring the stem in ventral view, the milky yellow green colour in life, the large size, with shoots up to 3 mm width and the regularly pinnate branching.

Description (from MEL2277389; NSW896415, 899756): Forming extensive opaque yellow green sheets of interwoven pendulous shoots on tree trunks and rocks, dark-brown in herbarium. Shoot systems regularly pinnate, dimorphic, with primary shoots 2.5–3 mm wide and up to 80 mm long, secondary shoots smaller in stature, typically 2–2.5 mm wide. Stems 280–330 µm diameter on primary shoots, with cortical cells in a single tier of 48–60 rows; cell walls brown pigmented, with heavy (very thick) but discontinuous secondary thickenings that constrict the cell lumen. Medullary cells in 140–160 rows; cell walls yellow pigmented, heavily

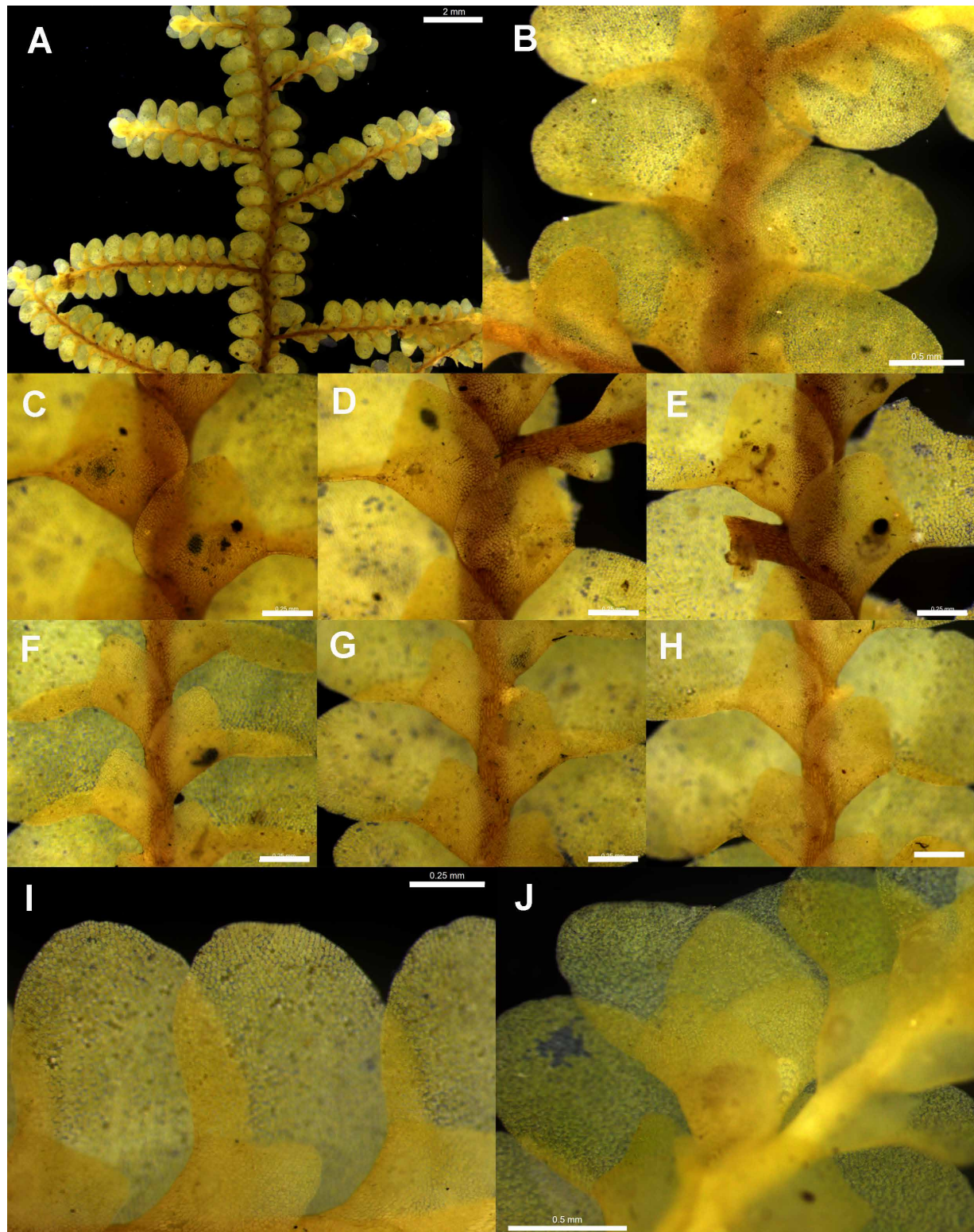


Fig. 5. *Radula oreopsis* Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 µm). C-E: Primary shoot lobules (250 µm). F-H: Secondary shoot lobules (250 µm). I: Secondary shoot lobe margins (250 µm). J: Female bracts (500 µm). A-I from NSW896698, J from NSW896415.

but discontinuously thickened by coarse nodular trigones, occasionally confluent but thin walls common between thickenings, that constrict the cell lumen. Cortical cells on dorsal stem surface arranged in an oblique zig-zag on young shoot sectors, cell elongation somewhat obscuring this pattern in mature shoot sectors. Leaf insertion exceeding dorsal stem mid-line, insertion lines interlocking over two dorsal cortical cell rows; not attaining ventral stem mid-line, leaving two cell rows leaf-free. Leaf lobes on primary shoots ovate-falcate, 1370–1630 μm long by 810–1000 μm wide, on secondary shoots ovate, 970–1160, μm long by 600–750 μm wide, contiguous to weakly imbricate, acroscopic base plane, leaves weakly convex, interlocking over the dorsal stem surface, stem obscured in dorsal view; lobe margins irregular in outline but entire, the interior lobe margin ampliate, extending beyond opposite stem margin, at times sharply curved, minutely auriculate at base or not, antical margin shallowly curved then straight, exterior margin narrowly to broadly rounded, postical margin straight, to gently arched. Lobules on primary shoots one quarter to one third of lobe area, broadly and asymmetrically rhombiform, 750–920 μm long by 630–740 μm wide, keel shallowly arched, angle between keel and stem 135° , keel turning through $45\text{--}90^\circ$ at apex, interior free margin ampliate, curvature more or less continuous from apex, gentle at first, increasing toward base, though occasionally antical margin straight for short distance, lobule apex obtuse; attached to stem along 0.25–0.3 of the interior margin, stem insertion straight, slightly arched at acroscopic end; with three papillae, one at the apex, two on the interior margin, one situated just below the midpoint of the interior lobule margin, the other immediately above the stem insertion; on secondary shoots smaller than lobules on primary shoots, one fifth to one quarter the lobe area, symmetrically to asymmetrically rhombiform, 600–760 μm long by 340–540 μm wide, keel straight to shallowly arched, angle between keel and stem 135° , keel turning through $45\text{--}55^\circ$ at the apex, interior free margin curved to weakly ampliate, apex obtuse. Leaf lobe cells rotund to rounded-oblong, 21–27 μm long, 17–22 μm wide, thin walled with concave to triangular trigones, medial wall thickenings absent; cells of lobe margin smaller than those of leaf middle, quadrate to rectangular, 14–20 μm long by 13–16 μm wide, long axis orientated parallel to lobe margin, exterior cell walls slightly thickened medially, thickening projecting

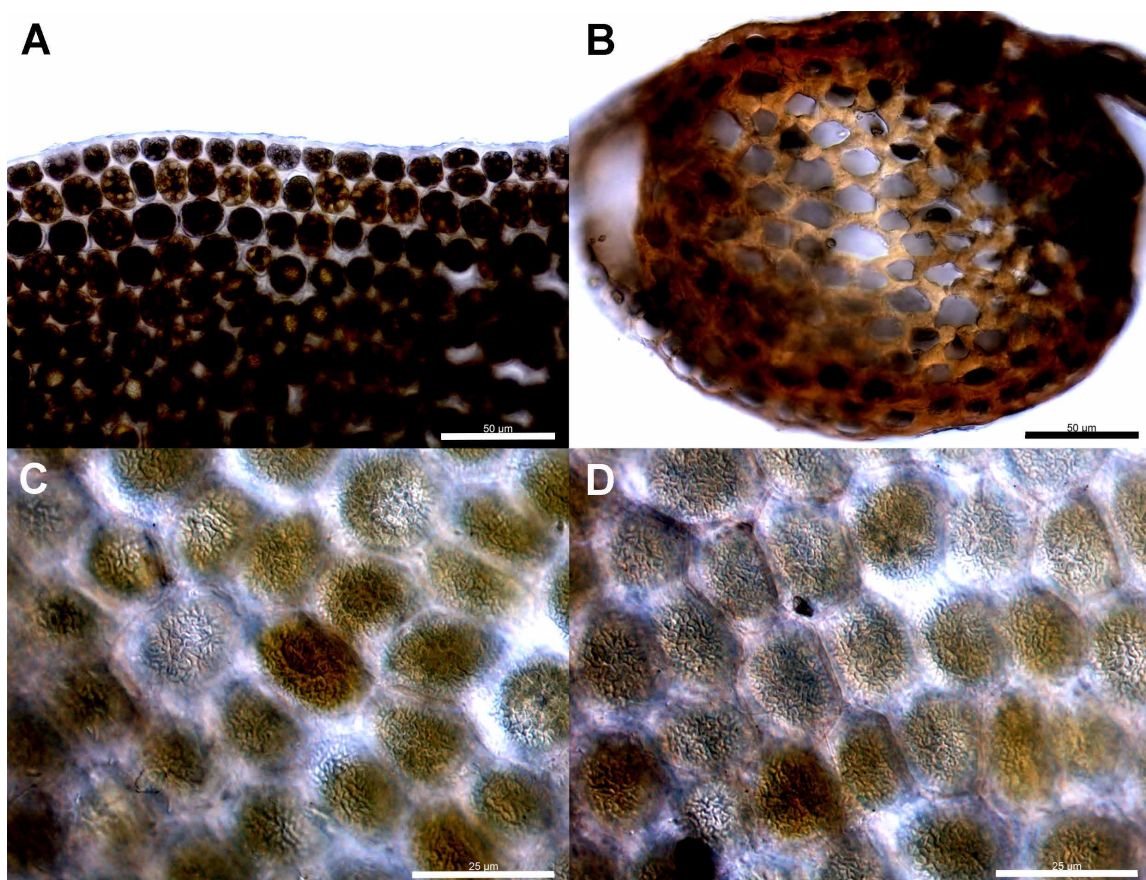


Fig. 6. *Radula oreopsis* Plate B. A: Leaf-lobe margin (50 μm). B: Transverse section of primary stem (50 μm). C, D: Leaf-lobe medial cell surface, showing ruminate ornamentation (25 μm). All from NSW896698.

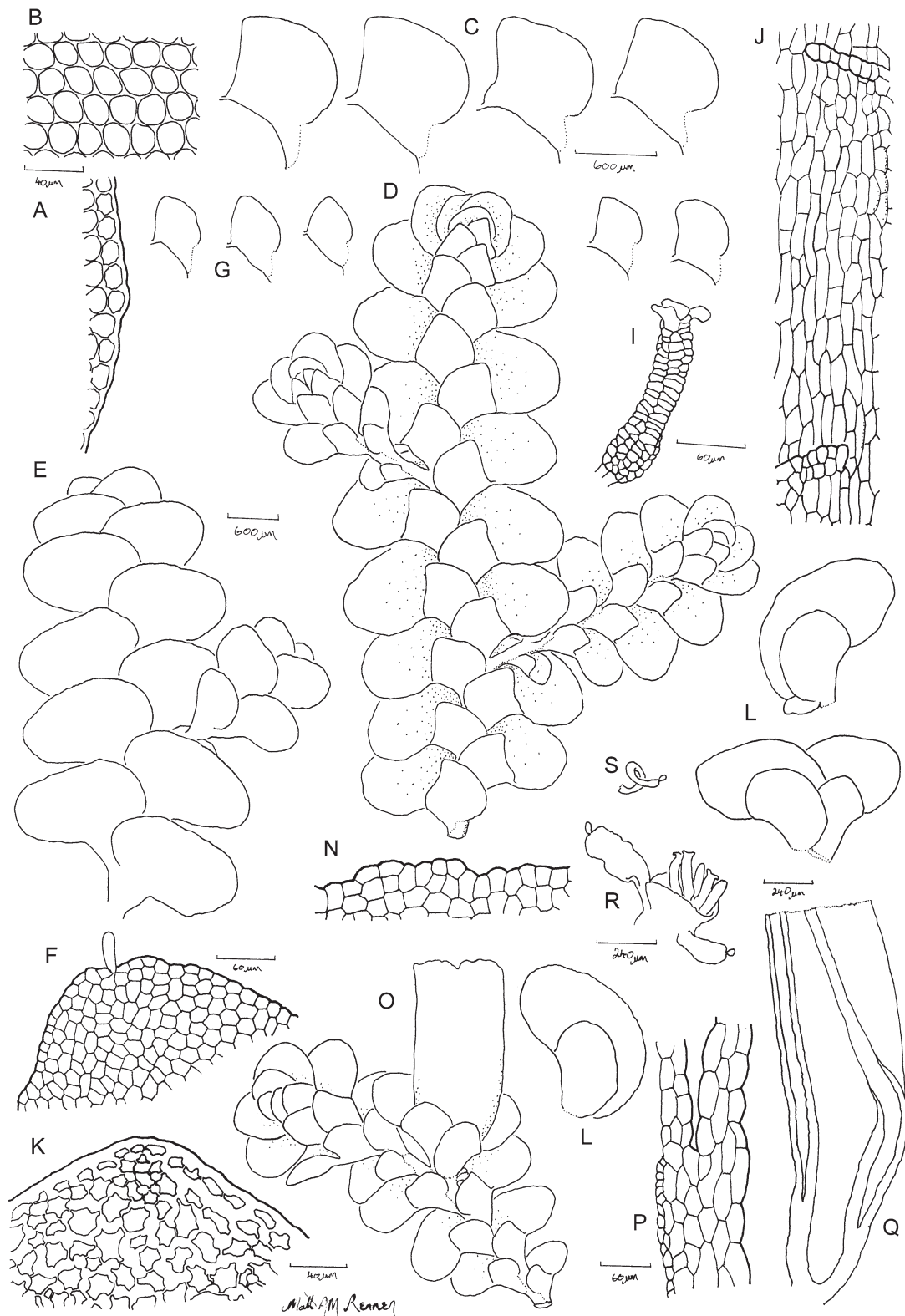


Fig. 7. *Radula oreopsis* Line drawings. A: Lobe marginal cells. B: Lobe medial cells. C: Four lobules from primary shoots. D: Ventral view of primary shoot. E: Dorsal view of primary shoot. F: Lobule apex. G: Five lobules from secondary branches. I: Archegonium. J: Cells on dorsal stem surface. K: Transverse stem section. L: One separated and one unseparated pair of female bracts. N: Cell detail of perianth mouth. O: Perianth bearing shoot. P: Longitudinal section of perianth-perigynium junction. Q: Longitudinal section of perianth. R: archegonia on gynoecial disc encompassed by protoperianth and flanked by two micro-bracts. S: An abbreviated micro-bract.

outward so margin is indistinctly crenulate. Cell surface with ruminant ornamentation, bearing ridges with irregular profile and size that impart an irregular, eroded honeycomb appearance to the surface. Oil-bodies not known. Asexual reproduction by caducous leaves, leaf-lobes fragmenting into irregular pieces until entire lobe dislocated, older shoot sectors sometimes devoid of leaf-lobes. Dioicous. Androecia not seen. Gynoecia terminal on axes, with one pair of female bracts subtended by typically one but occasionally two full-sized subfloral innovations that may again be fertile. Archegonia 160–200 μm tall, archegonia neck of 5 cell tiers, cells regularly arranged, 17–20 per gynoecium situated on a small raised disc of tissue encompassed by the base of the protoperianth. A pair of highly reduced accessory gynoecial bracts present, attached to the lateral sides of the disc immediately outside the protoperianth, typically ovate, 25 cells high and 10–15 cells wide, occasionally filiform, two cell tiers wide and spirally twisted, apex bearing a single papilla. Normal gynoecial bracts in one pair subequal, ovate-falcate, lobes 1300–1570 μm long by 890–940 μm wide, lobules subreniform, one third the lobe area, apex broadly rounded to obtuse, keel arched, insertion interlocking both dorsally and ventrally, insertion equitant. Perianth to 4000 μm long, to 1200 μm wide at mouth, mouth entire but outline irregular, parallel sided for upper three quarters, narrowing to a tubular low stem perigynium. Perianth walls bi- or tristratose at junction with calyptra, becoming unistratose above but with bistratose bands extending up to half way up perianth, increasing in width toward base. Low stem perigynium present, 5 or 6 stratose, cell walls heavily thickened and brown-pigmented, perianth-calyptra fusion elevated above female bracts on about 10 tiers of cells. Calyptral perigynium present, 5-stratose at base, strata progressively lost, unistratose above, unfertilised archegonia elevated on surface of calyptra.

Figs 5–7.

Etymology: Mountain-like, in reference to the surface ornamentation on leaf-lobe cells.

Distribution and ecology: Endemic to Australia, where known from the Wet Tropics Bioregion of north-eastern Queensland. Occurs between around 100 and 900 m asl as an epiphyte on tree trunks and branches or a lithophyte on the sides of large boulders within forest. *Radula oreopsis* is not uncommon in the Wet Tropics, and can be a conspicuous component of the non-vascular plant community in some forests, where it forms extensive, often pure, milky yellow-green sheet-like wefts that hang loosely from vertical surfaces. Shoots, particularly older sectors, are often host to a range of micro-species belonging to the Lejeuneaceae, including *Cololejeunea* and *Drepanolejeunea*. It may occur admixed with *R. javanica*, *R. jovetiana*, *R. loriana*, *R. mittenii*, and *R. myriopoda*, and a cornucopia of other large sylvestral bryophytes.

Identification: *Radula oreopsis* is a fairly distinctive species that can be recognized in the field with care. Its outstanding feature is the ruminant ornamentation on the leaf-lobe cell surface. So far as is known, ruminant ornamentation is unique to *R. oreopsis*, and therefore distinguishes it from all other species with which it could be confused (and there are many). While best viewed under 1000 \times magnification, the ornamentation imparts a milky-yellow colouration to living plants which while distinctive and observable in the field, is not unique. Living plants of *Radula mittenii* Steph., another Australian species with ornamented leaf-lobe cell surfaces are also milky-yellow in life. *Radula oreopsis* can be distinguished from *R. mittenii* by lobule shape and spacing, which are broadly and asymmetrically rhombiform with an ampliate interior margin, a stem-insertion 0.25–0.3 \times the interior length, an exterior margin inclined toward the stem, and an antical margin inclined in *R. oreopsis*. In *R. mittenii* the lobules on primary shoots are more or less quadrate, attached to stem along 0.4–0.5 \times the interior length, the exterior margin is more or less parallel to stem and the antical margin is more or less perpendicular to it.

Radula oreopsis is superficially similar to *R. sharpii* K.Yamada from Papua New Guinea, however is readily differentiated by the leaf cell surface ornamentation, ruminant in *R. oreopsis*, rugose in *R. sharpii*. Lobule shape exhibits subtle differences, a small auricle is present on the lobule of *R. sharpii* at the lobe-lobule junction, such that the lobule margin extends postical of the lobe margin at the junction. The lobe-lobule junction of *R. oreopsis* does not have this feature.

Remarks: Most Australian specimens of *R. oreopsis* collected prior to this study were not ascribed to any species, however several specimens collected by Hicks in the Mossman Gorge were the basis of Yamada's Australian record of *R. sharpii*.

Specimens examined: AUSTRALIA: QUEENSLAND: COOK: Daintree National Park: Mossman River Gorge, 16° 26' S 145° 16' E, 28 Jun 1983, W.B. Schofield 79961 & M.I. Schofield (BRI-AQ735495, 539968–539970; CANB619258, 672125.1; MEL2277389; NSW428041, 428043); Mossman River Gorge, 4 miles W of Mossman, 16° 28' S 145° 16' E, 19 Apr 1968, W.A. Weber B-31788 (CANB302185); Mossman Gorge Section, Mossman River, 16° 28' S 145° 13' E, 120 m, 12 August 1995, E.A. Brown 93/305, B.M. Weicek & K.L. Radford (NSW390567); Rex Creek, 16° 28' S 145° 19' E, 10 Jul 2005, M.A.M. Renner 2037 & E.A. Brown (NSW872742); 16° 28' 11" S 145° 19' 37" E, 105 m, 24 Mar 2012, M.A.M. Renner 6289, V.C. Linis & E.A. Brown (NSW896675); M.A.M. Renner 6292, V.C. Linis & E.A. Brown (NSW896681); Rex Creek, upstream from swing

bridge, 16° 28' 13" S 145° 19' 42" E, 105 m, 24 Mar 2012, *M.A.M. Renner 6280, V.C. Linis & E.A. Brown* (NSW896663); 16° 28' 12" S 145° 19' 37" E, 128 m, 24 Mar 2012, *M.A.M. Renner 6303, V.C. Linis, & E.A. Brown* (NSW896692); *M.A.M. Renner 6305, V.C. Linis & E.A. Brown* (NSW896694); *M.A.M. Renner 6309, V.C. Linis & E.A. Brown* (NSW896698); Lamb Range, 22 km NE of Atherton, Mt Haig Road, Kauri Creek, 17° 08' S 145° 36' E, 800 m, *H. Streimann 29866* (CANB8408221); Babinda Falls ('The Boulders'), 17° 20' S 145° 50' E, 26 Jun 1983, *W.B. Schofield 79818 & M.I. Schofield* (BRI-AQ539972; MEL2279313, 2277365; NSW428040); Wooroonooran National Park: South Johnston River, McMillan Creek catchment, Gorrell Track c. 2 km S of South Johnston River picnic area (old forestry camp), 17° 40' 19" S 145° 43' 38" E, 600 m, 6 Apr 2013, *M.A.M. Renner 6562, V.C. Linis & E.A. Brown* (NSW970433); 17° 40' 26" S 145° 43' 58" E, 600 m, 6 Apr 2012, *M.A.M. Renner 6572, V.C. Linis & E.A. Brown* (NSW970425); *M.A.M. Renner 6574, V.C. Linis & E.A. Brown* (NSW970428); South Johnston River catchment, Gorrell Track, 17° 40' 32" S 145° 44' 18" E, 560 m, 6 Apr 2012; *M.A.M. Renner 6581, V.C. Linis & E.A. Brown* (NSW970377); South Johnston River catchment, Maple Creek, Maple Creek Road, 17° 42' 06" S 145° 40' 22" E, 600 m, 5 Apr 2012, *M.A.M. Renner 6543, E.A. Brown & V.C. Linis* (NSW899756); **NORTH KENNEDY:** Tully Gorge State Forest, 17° 45' S 145° 39' E, 300 m, 2 August 1995, *E.A. Brown 95/136, B.M. Wiecek & K.L. Radford* (NSW390395).

Radula javanica Gottsche *Synopsis Hepaticarum* 2: 257. 1845

Type: Caroline Islands, Kusaie (Ualan) Island, 1825, *Strong*, comm. by R.P. Lesson, lectotype (designated by Castle (1966): in *Herb. Gottsche* (B); isolectotypes: ex *Herb. Bescherelle* (BM!), *Herb. Musc. Paris* (PC)

Radula cordiloba Taylor *Journal of Botany* 5: 375. 1846

Type: Pacific Isles, *T. Nightingale*, herb. Hooker (BM!).

Radula erigens (M.A.M. Renner & Braggins) M.A.M. Renner *syn. nov.*

Radula cordiloba Taylor subsp. *erigens* M.A.M. Renner & Braggins *Journal of the Hattori Botanical Laboratory* 97: 45. 2005

Type: New Zealand, Kermadec Islands, Raoul Island, 1956, *R. Cooper*. (holotype: AK44347 [ex AKU63120]! isotype: CHR!).

Morph 1: Rheophytic plants with reflexed lobule apices and copious caducous leaf production.

Description [from BRI-AQ722868]: Forming extensive pure sheets of interwoven pendulous shoots on rocks within and around waterways. Yellow-green in life, light-brown in herbarium. Shoot systems dimorphic, regularly pinnate, becoming irregularly bipinnate and densely branched with age, primary shoots 1.2–2 mm wide and up to 60 mm long, secondary shoots smaller in stature. Stems 250–310 µm diameter on primary shoots, with cortical cells in a single tier of 44–52 rows, cell walls yellow-brown pigmented, heavily and continuously thickened, thickenings constricting the cell lumen; medullary cells in 104–120 rows, cell walls yellow-pigmented, heavily and continuously thickened by confluent coarse nodular trigones that partially constrict the cell lumen, thin walls rare between thickenings. Cortical cells on dorsal stem surface arranged in an oblique zig-zag on young shoot sectors, cell elongation somewhat obscuring this pattern in mature shoot sectors. Leaf insertion exceeding dorsal stem mid-line, insertion lines interlocking over two dorsal cortical cell rows. Leaf lobes broadly elliptical, 790–880 µm long by 510–660 µm wide on primary shoots, 540–750 µm long by 410–550 µm wide on secondary shoots, remote to contiguous, acroscopic base not sharply deflexed away from stem, leaves flat to weakly convex, not interlocking over the dorsal stem surface, stem visible between leaf lobes in dorsal view, margins irregular, entire to crenulate due to slightly bulging marginal cells, bearing marginal rhizoids, the interior lobe margin curved, not auriculate, antical margin shallowly curved, exterior margin broadly rounded, postical margin gently curved or substraight. Lobules on primary shoots subquadrate, typically one twelfth to one sixth the lobe area, 380–645 µm long by 340–535 µm wide, keel straight or shallowly arched except at apex, closely pressed against the stem at the base, angle between keel and stem 160–180°, keel abruptly turning through 90–100° at the apex, interior margin free for two thirds its length, free portion ampliate, acroscopic margin straight or shallowly sigmoidally curved, inclined to shoot axis, apex obtuse; lobe-lobule junction antical to acroscopic end of stem insertion; lobules on mature shoot sectors have the free apical portion markedly reflexed along the line between the lobe-lobule junction and the top of the stem insertion, the reflexed portion pointing backward and outward from the shoot axis; attached to stem along 0.3–0.4 of the interior margin, stem insertion S-shaped, not or gently revolute at acroscopic end; lobule apex bearing a single papilla, with another papilla situated on the interior lobule margin above the stem insertion; lobules on primary shoots larger, with more ampliate free interior margins, and more pronounced deflexion than those on secondary shoots. Lobules on secondary shoots rhomboid, one twelfth to one ninth the lobe area, keel shallowly curved, straight or shallowly arched angle between keel and stem 135°, keel turning through 45–55° at the apex, interior free margin not ampliate, acroscopic margin curved or S-shaped, inclined to shoot axis, apex obtuse to acute. Leaf lobe cells subquadrate to rounded-oblong, irregularly arranged and of mixed sizes, 12–23 µm long by 12–17 µm wide, thin walled with small concave trigones, medial wall thickenings absent; cells of lobe margin smaller than those of mid-lobe, quadrate to rotund, 9–15 µm long and wide, exterior cell

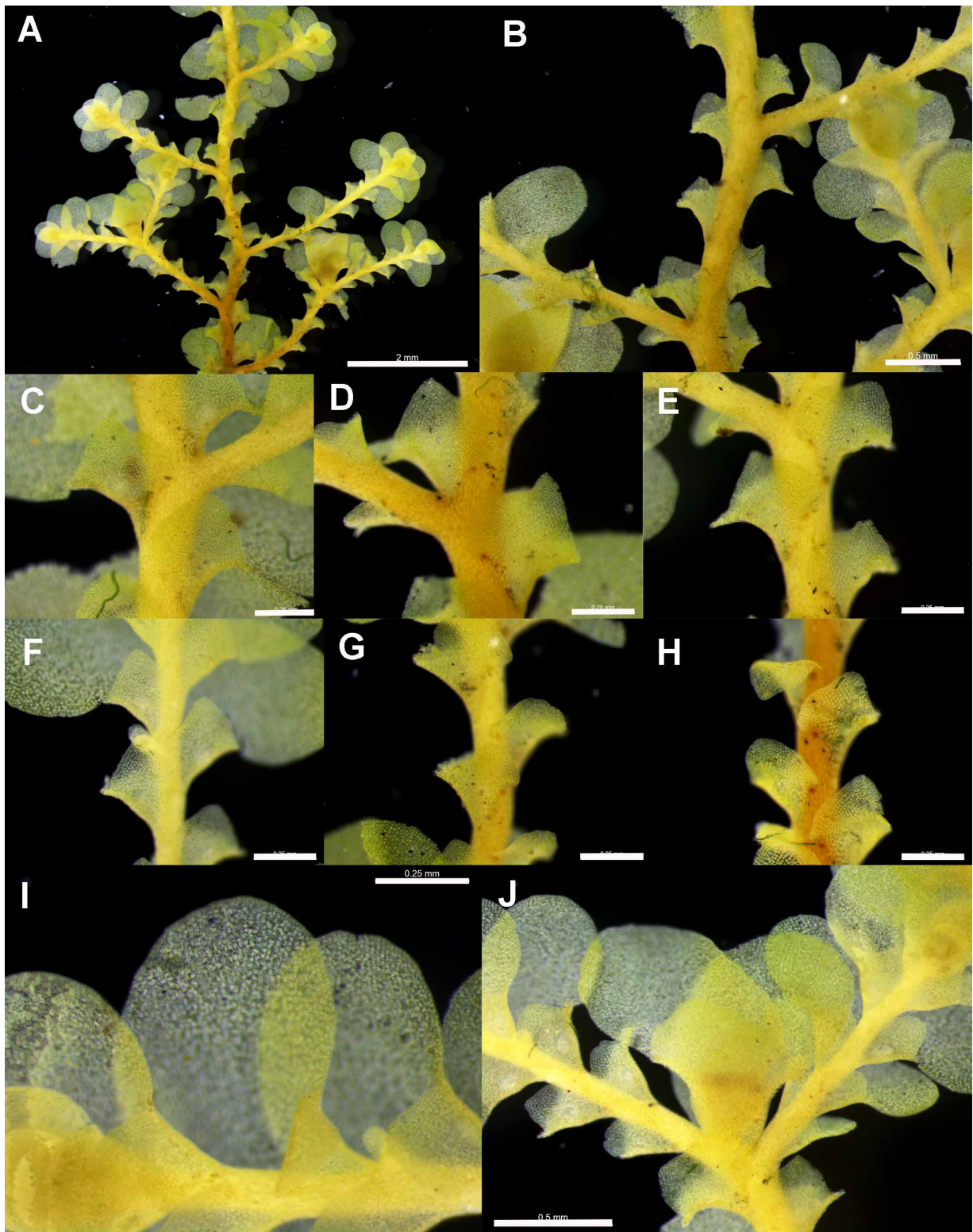


Fig. 8. *Radula javanica* rheophytic morph Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μm). C-E: Primary shoot lobules (250 μm). F-H: Secondary shoot lobules (250 μm). I: Secondary shoot lobe margins (250 μm). J: Female bracts (500 μm). All from NSW978121.

walls not thickened bulging medially, imparting weakly crenulated appearance to lobe margin. Leaf lobe cell surface weakly bulging, bearing punctulate ornamentation. Oil-bodies not known. Asexual reproduction by caducous leaf lobes, shed shortly after leaf maturation, older shoot sectors on leading stems and branches totally devoid of leaf-lobes, leaf lobes apparently dislocating whole, fragmentation scars jagged but regular, shoot primordia not forming as irregular buds on leaf lobe prior to dislocation, but marginal rhizoids are produced before dislocation. Dioicous. Androecia on indeterminate branches that continue vegetative growth, androecial bracts in 4–8 pairs, lobules epistatic, keel deeply curved, bucket-like, free apical portion triangular, apex obtuse, moderately deflexed, lobes rounded, usually caducous, antheridia not seen. Gynoecia terminal on branches, never produced from leading shoots, with one pair of female bracts subtended by one or two full sized subfloral innovations that are again fertile. Where a single subfloral innovation is present, a ‘resting’ shoot primordium occurs in place of the second subfloral innovation. Archegonia 160–200 μm tall, archegonia neck seven to eight cell tiers, 14–15 per gynoecium on a small raised disc of tissue encompassed by the base of the protoperianth surrounding archegonia. Female bracts in one pair, subequal, elliptic-falcate, lobes 730–1040 μm long by 410–530 μm wide, lobules oblong-falcate, one half the lobe area, apex rounded, keel weakly to strongly arched, insertion interlocking dorsally, insertion equitant. Perianth walls unistratose above, with bistratose bands extending from half way up perianth, increasing in width and becoming confluent toward the perianth base, perianth walls progressively increasing in thickness toward base where 2 or 3 stratose; low stem perigynium present, 5–6 stratose, cell walls heavily thickened and brown-pigmented, perianth-calyptra fusion elevated above female bracts on 9–15 tiers of cells; calyptral perigynium present, 2–4 stratose at base, strata progressively lost, unistratose above, unfertilised archegonia elevated on surface of calyptra.

Figs 8–10

Morph 2: Lithophytic plants in forest or streamsides with reflexed lobule interior margin and apex.

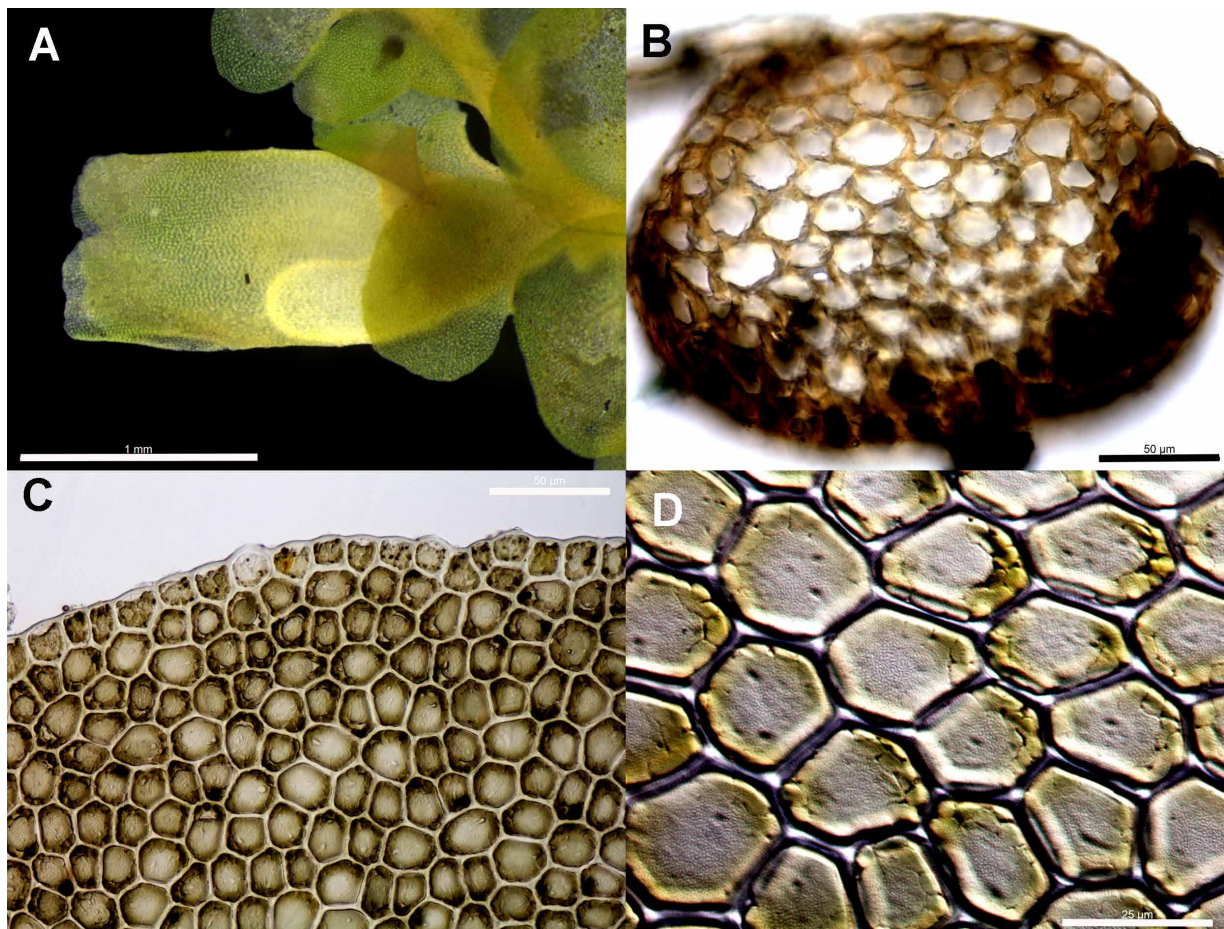


Fig. 9. *Radula javanica* rheophytic morph Plate B. A: Ventral view of perianth (1 mm). B: Transverse section of primary stem (50 μm). C: Leaf-lobe margin (50 μm). D: Leaf-lobe medial cell surface, showing rugose ornamentation (25 μm). All from NSW978121.

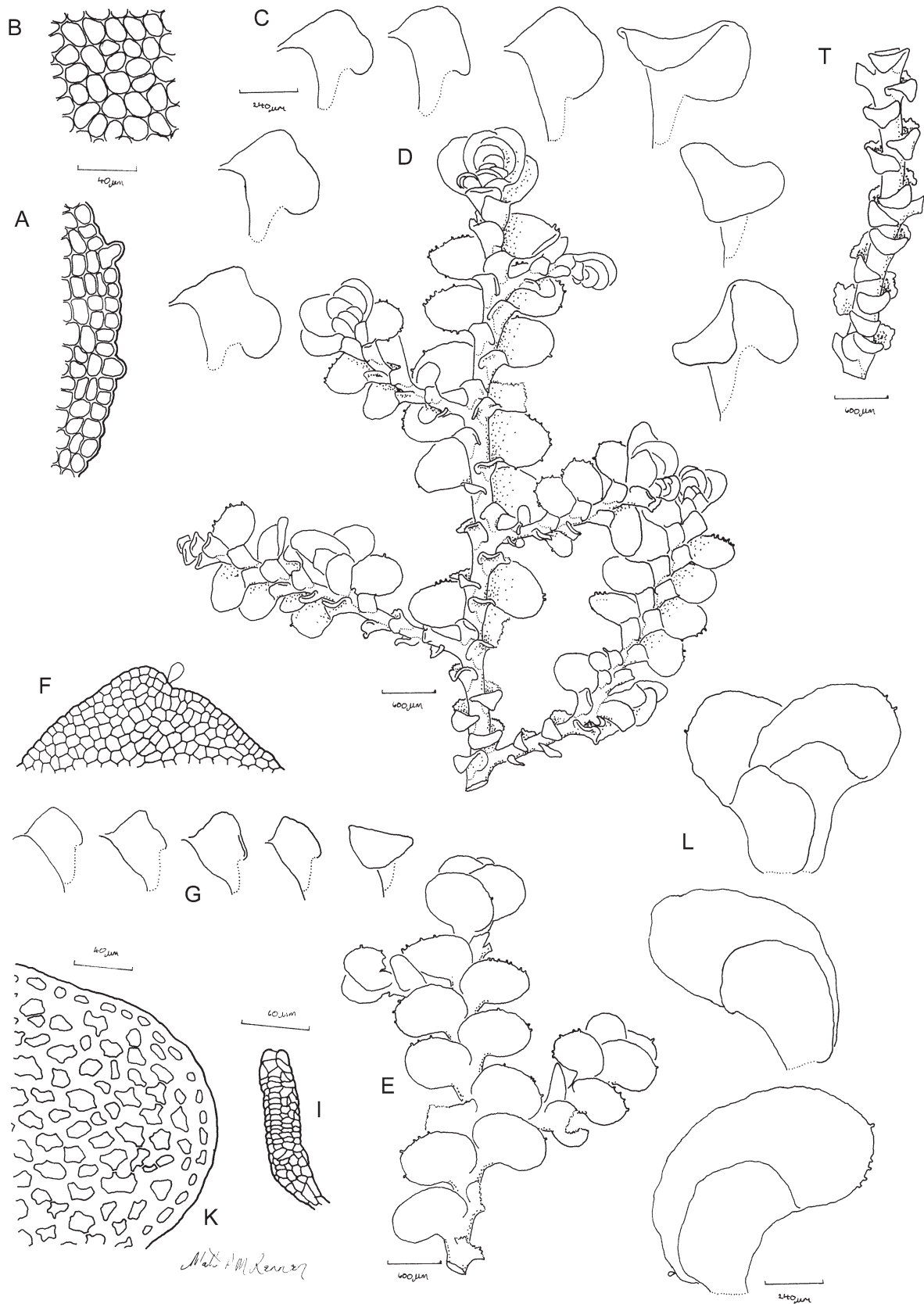


Fig. 10. *Radula javanica* rheophytic morph Line drawings. A: Lobe marginal cells. B: Lobe medial cells. C: Eight lobules from primary shoots. D: Ventral view of primary shoot. E: Dorsal view of primary shoot. F: Lobule apex. G: Five lobules from secondary branches. I: Archegonium. J: Cells on dorsal stem surface. K: Transverse stem section. L: One separated and one unseparated pair of female bracts. T: Mature sector of primary shoot showing recurved lobule apices. All from NSW978121.

above the stem insertion; lobules on primary shoots larger, with more ampliate free interior margin and more pronounced reflexion and undulation than those on secondary shoots; lobules on branches rhomboid, one seventh to one sixth the lobe area, keel shallowly arched, angle between keel and stem 135° , keel turning through 45° , interior free margin not ampliate, variously reflexed from apex to base of interior free margin in one or two bites, in part or in full so as to point backward along shoot axis, apex obtuse to acute. Leaf lobe cells rounded-oblong, regularly arranged in loose rows, unequally sized, $16\text{--}34\ \mu\text{m}$ long by $12\text{--}16\ \mu\text{m}$ wide, thin walled with triangular trigones, medial wall thickenings absent; cells of lobe margin smaller than those of leaf middle, quadrate to rectangular, $9\text{--}15\ \mu\text{m}$ long and wide, exterior cell walls not thickened, cell lumen not bulging medially. Leaf lobe cell surface weakly bulging, bearing punctulate ornamentation. Oil-bodies not known. Asexual reproduction by caducous leaf lobes, sporadic, shoots progressively losing leaf-lobes through fragmentation, older shoot sectors on leading stems and branches may be totally devoid of leaf-lobes but some leaf-lobes may be retained, leaf-lobes typically tearing into several pieces, fragmentation scars jagged, irregular, typically leaving part of basiscopic leaf margin attached beyond keel, shoot primordia not forming as irregular buds on leaf lobe prior to leaf dislocation. Dioicous. Androecia on indeterminate branches that continue vegetative growth, androecial bracts in 4–8 pairs, lobules epistatic, keel deeply curved, bucket-like, free apical portion triangular, apex obtuse, moderately deflexed, lobes rounded, not usually caducous, antheridia not seen. Gynoecia terminal on branches, never produced from leading shoots, subtended by one or two full sized subfloral innovations that are again fertile. Where a single subfloral innovation is present, a ‘resting’ shoot primordium occurs in place of the second subfloral innovation. Archegonia $160\text{--}210\ \mu\text{m}$ tall, archegonia neck seven to eight cell columns, $16\text{--}25$ per gynoecium on a small raised disc of tissue, not encompassed by the protoperianth, protoperianth absent. Female bracts in one pair, asymmetrical, elliptic-ovate, larger lobe $940\text{--}1090\ \mu\text{m}$ long by $510\text{--}640\ \mu\text{m}$ wide, smaller lobe $880\text{--}1010\ \mu\text{m}$ long by $460\text{--}590\ \mu\text{m}$ wide, lobules oblong-falcate, one third to one half the lobe area, apex rounded or obtuse, keel arched to curved, insertion interlocking dorsally and ventrally, insertion equitant. Perianths $4200\text{--}4700\ \mu\text{m}$ long and $1050\text{--}1200\ \mu\text{m}$ at mouth, mouth irregularly lobed, parallel sided for upper two thirds, widening to a faint bulb in basal third, broadest in middle of this bulb $1200\text{--}1350\ \mu\text{m}$ wide, then tapering to base. Perianth walls unistratose above, with bistratose bands extending from half way up perianth, increasing in width and becoming confluent toward the perianth base, perianth walls progressively increasing in thickness toward base where 2–3 stratose; low stem perigynium present, 5–6 stratose, cell walls heavily thickened and brown-pigmented, perianth-calyptra fusion elevated above female bracts on 9–15 tiers of cells; calyptral perigynium present, 2–4 stratose at base, strata progressively lost, unistratose above, unfertilised archegonia elevated on surface of calyptra.

Fig 11–14

Morph 3: Epiphytic or lithophytic plants in forest, with more or less flat lobules.

Description [AK323601]: Forming extensive pure sheets of interwoven pendulous shoots on tree and palm trunks and on rocks. Live plants mid to dark green, brown in herbarium. Shoot systems dimorphic, regularly pinnate, becoming irregularly bipinnate in older sectors, with primary shoots $1.9\text{--}2.8\ \text{mm}$ wide and up to $80\ \text{mm}$ long, secondary shoots smaller in stature than primary shoots. Stems $350\text{--}500\ \mu\text{m}$ diameter on primary shoots, with cortical cells in a single tier of 40–60 rows, cell walls yellow-brown pigmented, heavily and continuously thickened, thickenings constricting the cell lumen; medullary cells in 95–160 rows, cell walls yellow-pigmented, heavily and continuously thickened by confluent coarse nodular trigones that partially constrict the cell lumen, thin walls rare between thickenings. Cortical cells on dorsal stem surface arranged in straight longitudinal row on young and mature shoot sectors. Leaf insertion exceeding dorsal stem mid-line, insertion lines interlocking over two dorsal cortical cell rows, insertion not attaining the ventral stem mid-line, leaving one or two ventral cortical cell rows leaf-free. Leaf lobes elliptic-oblong, sometimes very slightly ovate, $1300\text{--}1530\ \mu\text{m}$ long by $740\text{--}1050\ \mu\text{m}$ wide on primary shoots, $820\text{--}1290\ \mu\text{m}$ long by $575\text{--}790\ \mu\text{m}$ wide on secondary shoots, imbricate, acroscopic base not sharply deflexed away from stem, flat to weakly convex, interlocking over the dorsal stem surface, stem not visible in dorsal view, margins entire, the interior lobe margin curved, reaching and usually extending slightly beyond opposite stem margin, not auriculate, antical margin shallowly curved to straight in the outer half, exterior margin rounded, postical margin gently curved or substraight. Lobules on primary shoots subquadrate, one sixth to one fifth the lobe area, $580\text{--}940\ \mu\text{m}$ long by $450\text{--}700\ \mu\text{m}$ wide, keel straight to arched, angle between keel and stem 135° , keel turning through 90° mostly at the ends, interior lobule margin free for one half to two thirds its length, free portion ampliate, occasionally reflexed, on larger shoots fully covering stem, obscuring most of the stem in ventral view, acroscopic margin straight, usually inclined toward stem axis, not reflexed, apex obtuse, free exterior margin with a shallow undulation, the medial part of margin depressed; lobe-lobule junction approximately level with the acroscopic end of stem insertion, stem insertion shallowly S-shaped, gently revolute at acroscopic end; lobule apex bearing a single papilla, with another papilla situated on the interior lobule margin above the stem insertion; lobules on primary shoots larger, with more ampliate free interior margin and more pronounced

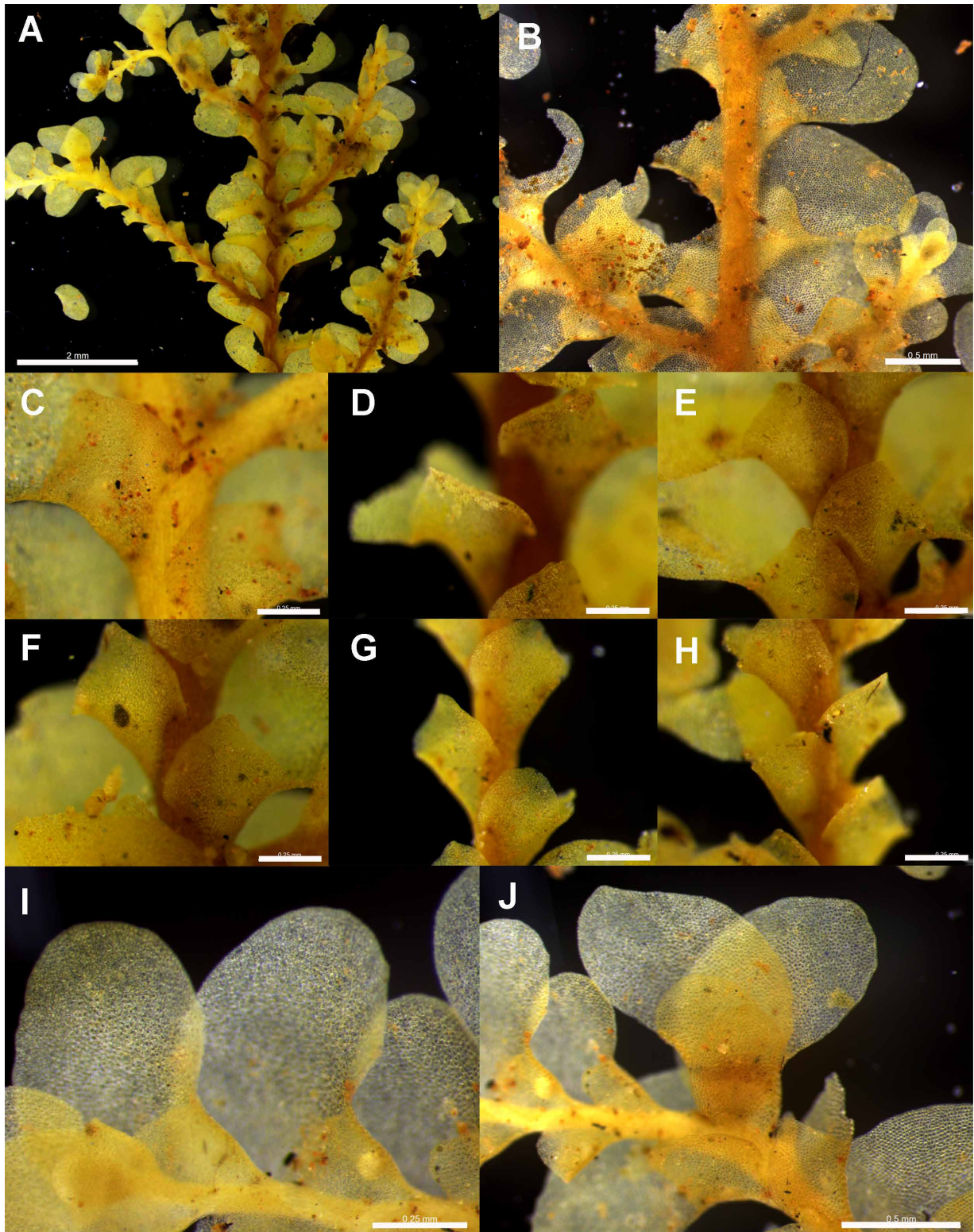


Fig. 11. *Radula javanica* epiphytic morph Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 µm). C-E: Primary shoot lobules (250 µm). F-H: Secondary shoot lobules (250 µm). I: Secondary shoot lobe margins (250 µm). J: Female bracts (500 µm). All from NSW896734.

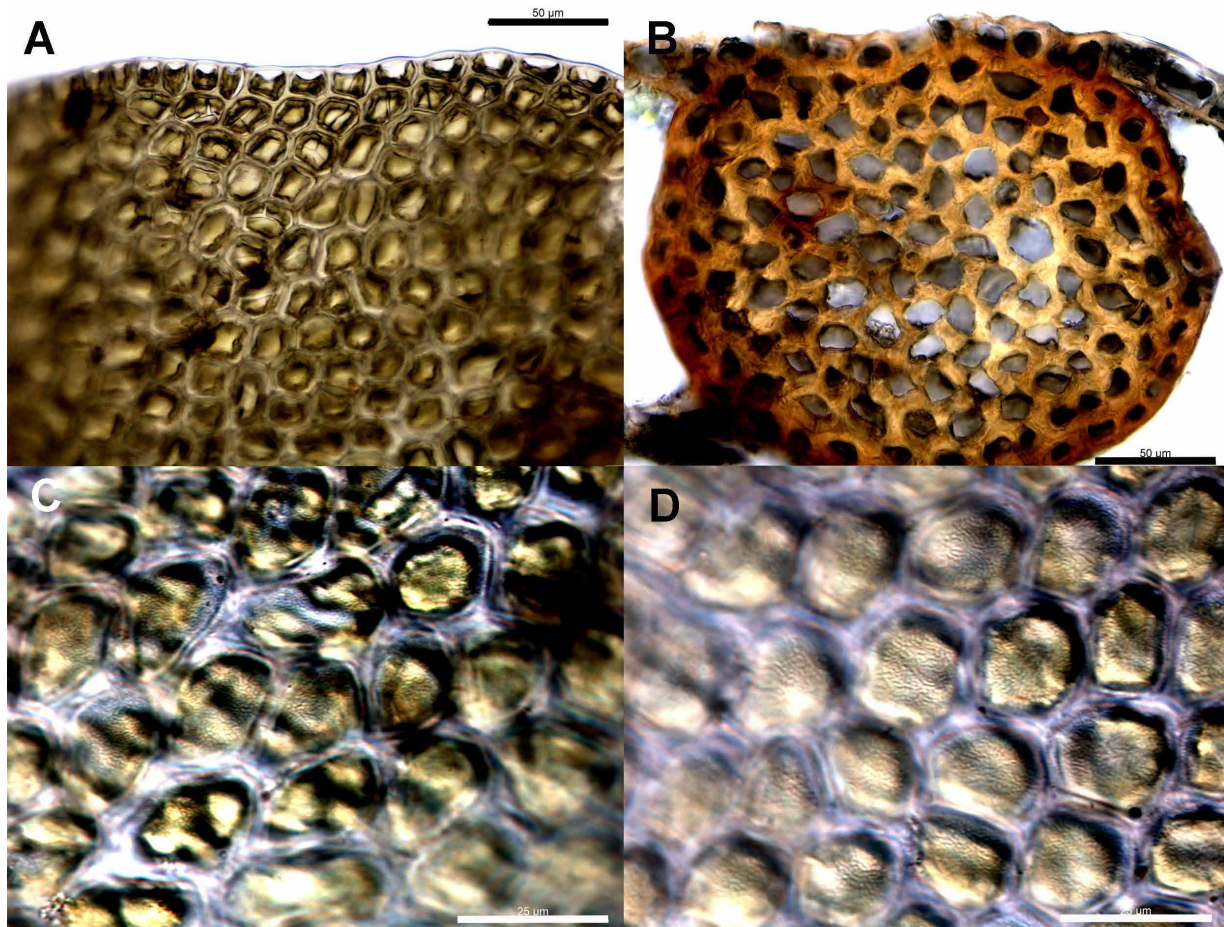


Fig. 12. *Radula javanica* epiphytic morph Plate B. A: Leaf-lobe margin (50 µm). B: Transverse section of primary stem (50 µm). C, D. Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). All from NSW896734.

Description [from MEL1037775]: Forming extensive pure sheets of interwoven pendulous shoots on tree trunks and rocks. Live plants mid to dark green, brown in herbarium. Shoot systems dimorphic, regularly pinnate, becoming irregularly bipinnate in older sectors, with primary shoots 1.6–2.5 mm wide and up to 80 mm long, secondary shoots smaller in stature than primary shoots. Stems 340–410 µm diameter on primary shoots, with cortical cells in a single tier of 45–58 rows, cell walls yellow-brown pigmented, heavily and continuously thickened, thickenings constricting the cell lumen; medullary cells in 97–135 rows, cell walls yellow-pigmented, heavily and continuously thickened by confluent coarse nodular trigones that partially constrict the cell lumen, thin walls rare between thickenings. Cortical cells on dorsal stem surface arranged in straight longitudinal row on young and mature shoot sectors. Leaf insertion exceeding dorsal stem mid-line, insertion lines interlocking over two dorsal cortical cell rows, insertion not attaining the ventral stem mid-line, leaving one ventral cortical cell row leaf-free. Leaf lobes elliptic-oblong, 1100–1320 µm long by 640–875 µm wide on primary shoots, 735–1140 µm long by 490–720 µm wide on secondary shoots, imbricate, acroscopic base not sharply deflexed away from stem, flat to weakly convex, interlocking over the dorsal stem surface, stem not visible in dorsal view, margins entire, the interior lobe margin curved, reaching or extending slightly beyond opposite stem margin, not auriculate, antical margin shallowly curved, exterior margin rounded, postical margin gently curved or substraight. Lobules on primary shoots subquadrate, one sixth to one fifth the lobe area, 510–595 µm long by 370–605 µm wide, keel arched, angle between keel and stem 135–165°, keel gradually turning through 60–90°, occasionally slight notch present at the apex, interior lobule margin free for one half to two thirds its length, free portion ampliate but not fully covering stem, margin reflexed in one or two ‘bites’, acroscopic margin curved, apical portion perpendicular to stem axis in larger lobules, occasionally reflexed along the apical margin only, or the upper half of the free portion of the lobule reflexed and pointing backward down the shoot axis, apex obtuse, free exterior margin with a single, deep undulation, the medial part of margin depressed, a distinct ‘knee’ present in outline above the lobe-lobule junction, lobules with an undulate exterior margin do not usually have the free portion of the lobule reflexed, though the margin only may be reflexed; lobe-lobule junction approximately level with the acroscopic end of stem insertion, attached to stem along 0.33–0.5 of the interior margin, stem insertion shallowly S-shaped, gently revolute at acroscopic end; lobule apex bearing a single papilla, with another papilla situated on the interior lobule margin

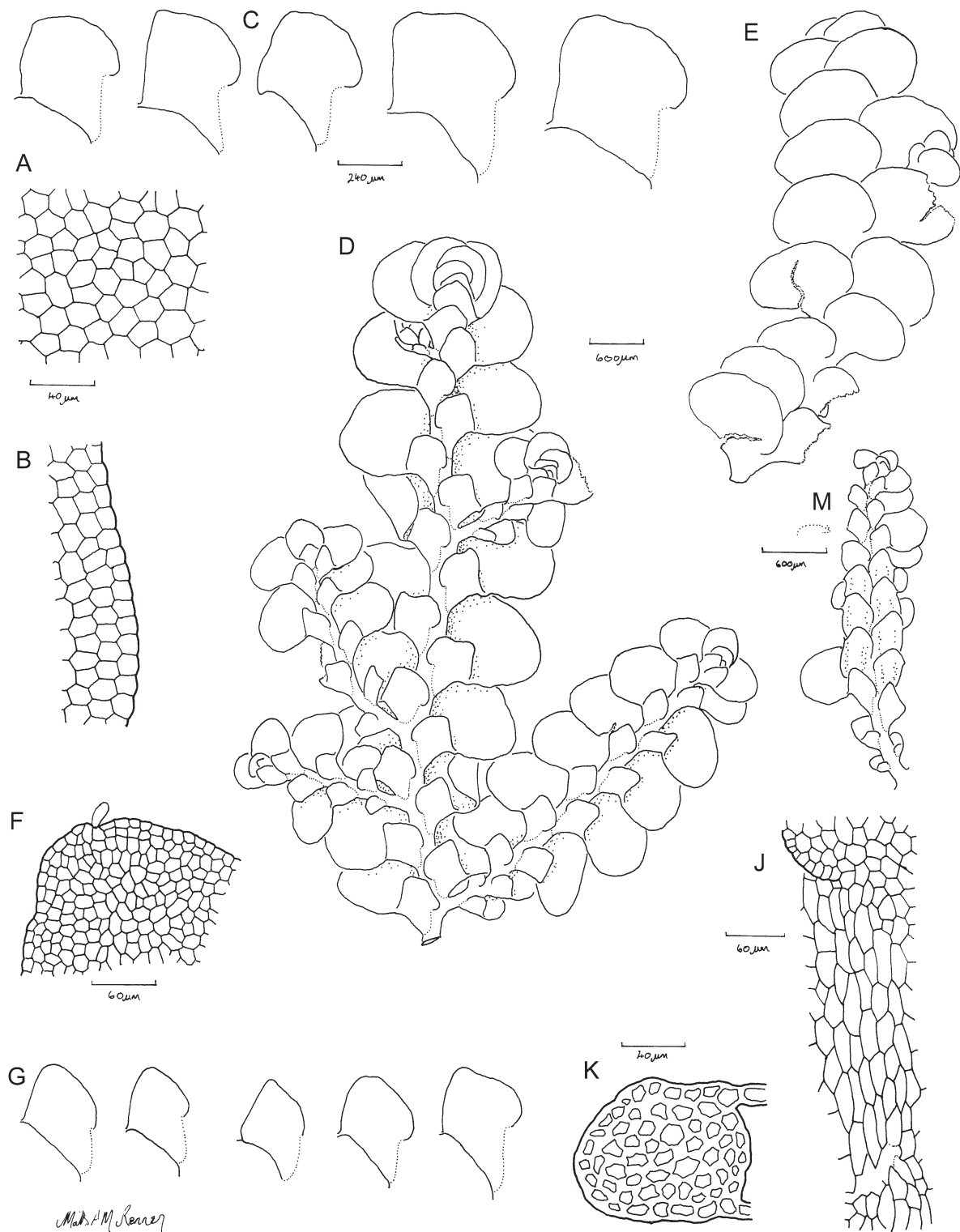


Fig. 13. *Radula javanica* epiphytic morph Line drawings A: Lobule marginal cells. B: Lobule medial cells. C: Five lobules from primary shoots. D: Ventral view of primary shoot. E: Dorsal view of primary shoot. F: Lobule apex. G: Five lobules from secondary branches. J: Cells on dorsal stem surface. K: Transverse stem section. M: Male shoot. All from MEL1037772.

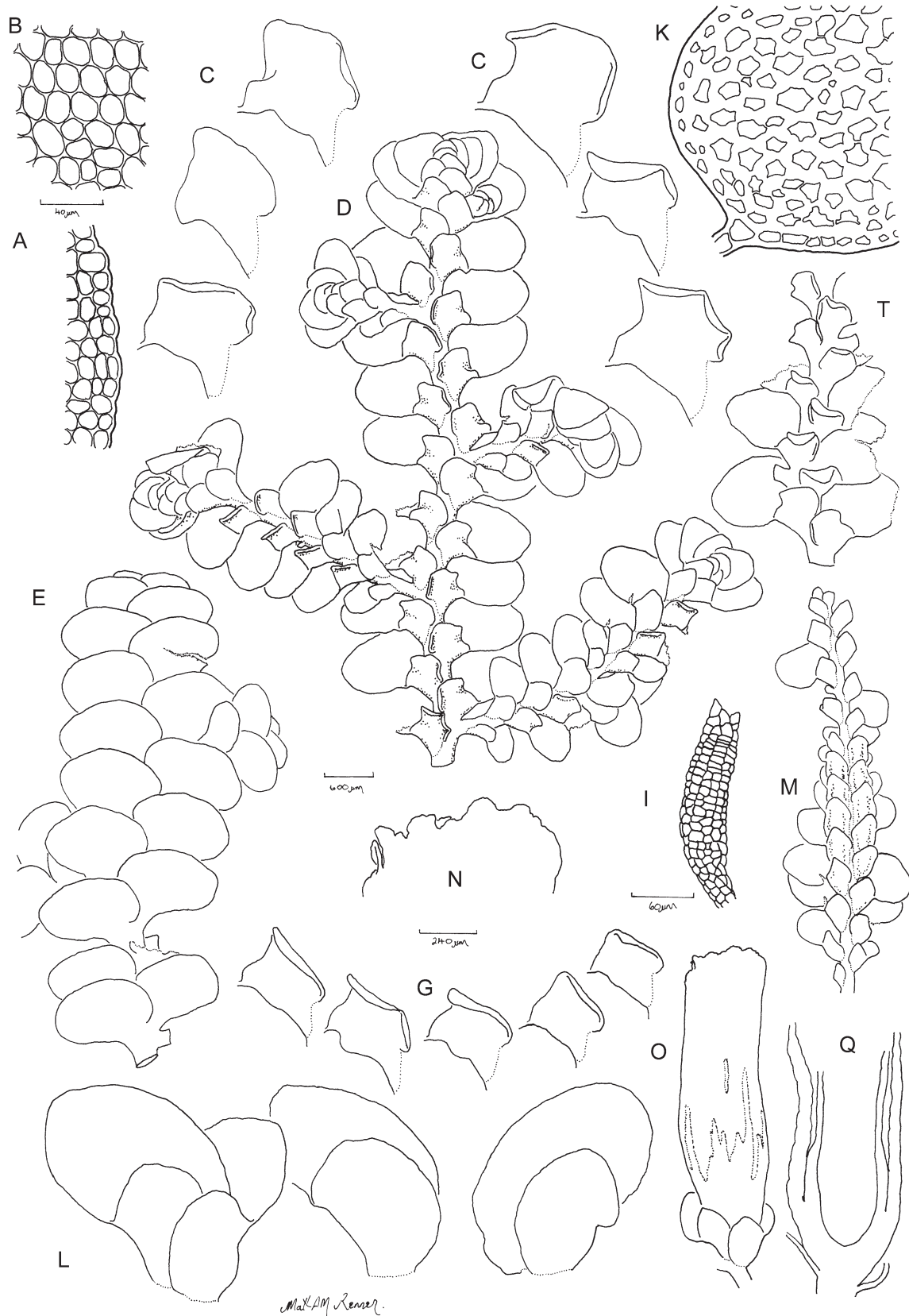


Fig. 14. *Radula javanica* lithophytic morph line drawings. A: Lobe marginal cells. B: Lobe medial cells. C: Six lobules from primary shoots. D: Ventral view of primary shoot. E: Dorsal view of primary shoot. G: Five lobules from secondary branches. I: Archegonium. K: Transverse stem section. L: One separated and one unseparated pair of female bracts. M: Male shoot. N: Perianth mouth. O: Perianth, showing basal bistratose bands. Q: Longitudinal section of perianth base. T: Mature sector of primary shoot showing recurved lobule apices. All from *Hicks 11506* (BRI).

reflexion and undulation than those on secondary shoots; lobules on secondary shoot quadrate to rhomboid, one sixth to one fifth the lobe area, 300–600 µm long by 230–440 µm wide, keel straight to shallowly arched, angle between keel and stem 135°, interior free margin weakly ampliate, not reflexed, apex obtuse. Leaf lobe cells rounded-oblong, regularly arranged in loose rows, unequally sized, 12–21 µm long by 10–13 µm wide, thin walled with triangular trigones, medial wall thickenings absent; cells of lobe margin smaller than those of leaf middle, quadrate to rectangular, 9–10 µm long and wide, exterior cell walls not thickened, cell lumen not bulging medially. Leaf lobe cell surface punctulate. Oil-bodies not known. Asexual reproduction by caducous leaf lobes, sporadic, leaf-lobes typically tearing into several pieces, fragmentation scars jagged, irregular, typically leaving part of basiscopic leaf margin attached beyond keel, shoot primordia not forming as irregular buds on leaf lobe prior to leaf dislocation. Dioicous. Androecia not seen. Gynoecia terminal on secondary branches, subtended by one or two full sized subfloral innovations that are again fertile. Where a single subfloral innovation is present, a ‘resting’ shoot primordium occurs in place of the second subfloral innovation. Archegonia c. 180 µm tall, archegonia neck seven or eight cell columns, c. 20 per gynoecium on a small raised disc of tissue, not encompassed by the protoperianth. Female bracts in one pair, asymmetrical, elliptic-ovate to slightly reniform, larger lobe 1060–1170 µm long by 590–650 µm wide, smaller lobe 800–1000 µm long by 520–600 µm wide, lobules oblong-falcate, one third to one half the lobe area, apex rounded or obtuse, keel arched to straight, insertion interlocking dorsally and ventrally. Perianths not seen.

Figs 15–17.

Distribution and ecology: Regionally *R. javanica* occurs in north-east Australia and throughout the Pacific, including the Kermadec Islands (New Zealand Botanical Region), New Caledonia, and at least as far east as Fiji. Within Australia *R. javanica* is distributed from the Wet Tropics Bioregion in north-east Queensland south to the coast to the north coast of north-east New South Wales, between c. 15° and 28° S latitude. *R. javanica* is generally found below about 400 m, in forest or scrub, and may grow as a lithophyte within waterways or within forest, sometimes in fairly dry situations, or as an epiphyte on tree trunks, branches or twigs.

Variation: The circumscription of *R. javanica* enforced upon this study makes it the most polymorphic species within the Australasian region. Individuals may appear very different from one another between habitats within regions. For example, on comparison between rheophytic individuals and forest-inhabiting individuals in both Australia and Fiji one is tempted to conclude that two species are present in both regions. This impression is reinforced by the fact that rheophytic individuals in both regions have the same morphology. As described above, plants differ in the size, shape and orientation of leaf-lobules, and the degree to which the margins and apex are reflexed. They also vary in their propensity to produce caducous leaf-lobes, with rheophytic individuals usually devoid of all but the youngest leaf-lobes, while forest inhabitants may retain all, or nearly all of theirs. Inter-individual variation within *R.* has been the source of some consternation for this author, and others similarly bemused by this species are in good company.

Identification: The polymorphism exhibited within the bounds of the circumscription accepted by this study is not a license for uncritical attribution of individuals to this species. Several features unify individuals of *R. javanica* as defined by this study:

1) the apex and/or interior lobule margin is usually reflexed to some degree; 2) the leaf lobe cell surfaces bear punctulate ornamentation, 3) the plants produce caducous leaves; 4) the shoot systems are pinnately branched. Determination of *R. javanica* a matter of firstly excluding from consideration similar species having distinctive characteristics, in Australia this involves comparison with *R. oreopsis* which is distinctive in its ruminant cell surface ornamentation; and *R. mittenii* which is distinctive in its quadrate, flat lobules. For more detail refer to the recognition sections of those two species (the latter published in Renner et al. 2013a).

Rheophytic plants are distinctive enough, having two outstanding features. Firstly the strongly deflexed lobules whose entire free apical portion points backward and outward from the shoot axis. The orientation of the deflexed lobules is due to the lobe-lobule junction lying antical to the acroscopic end of the lobule stem insertion line. Secondly the comprehensive dislocation of leaf-lobes from older sectors of both leading shoots and branches, denuding the shoot systems of *R. javanica* except for the few youngest pairs of leaves at each shoot apex. Rhizoids are often produced from the margins of leaves that have not yet fragmented.

Remarks: *Radula javanica* has been widely misunderstood in Australasia. Stephani (1889) recorded *R. reflexa* from Australia on the basis of a specimen from Rockingham Bay, collector unknown. The Dallacy collection in MEL is probably this specimen, or a duplicate of it. It is *R. javanica*. Yamada’s (1987) Australian record of *Radula reflexa* is also based on a mis-identification of *R. javanica*. Yamada’s (1984) record of *Radula multiflora* from Australia on the basis of two specimens collected by M.L. Hicks in Queensland. One of these is *Radula javanica*. Yamada’s (1987) Australian record of *Radula reflexa* is based on a mis-identification of *R. javanica*, as is his record of *R. multiflora*. Yamada also identified a specimen collected by G.A.M. Scott as

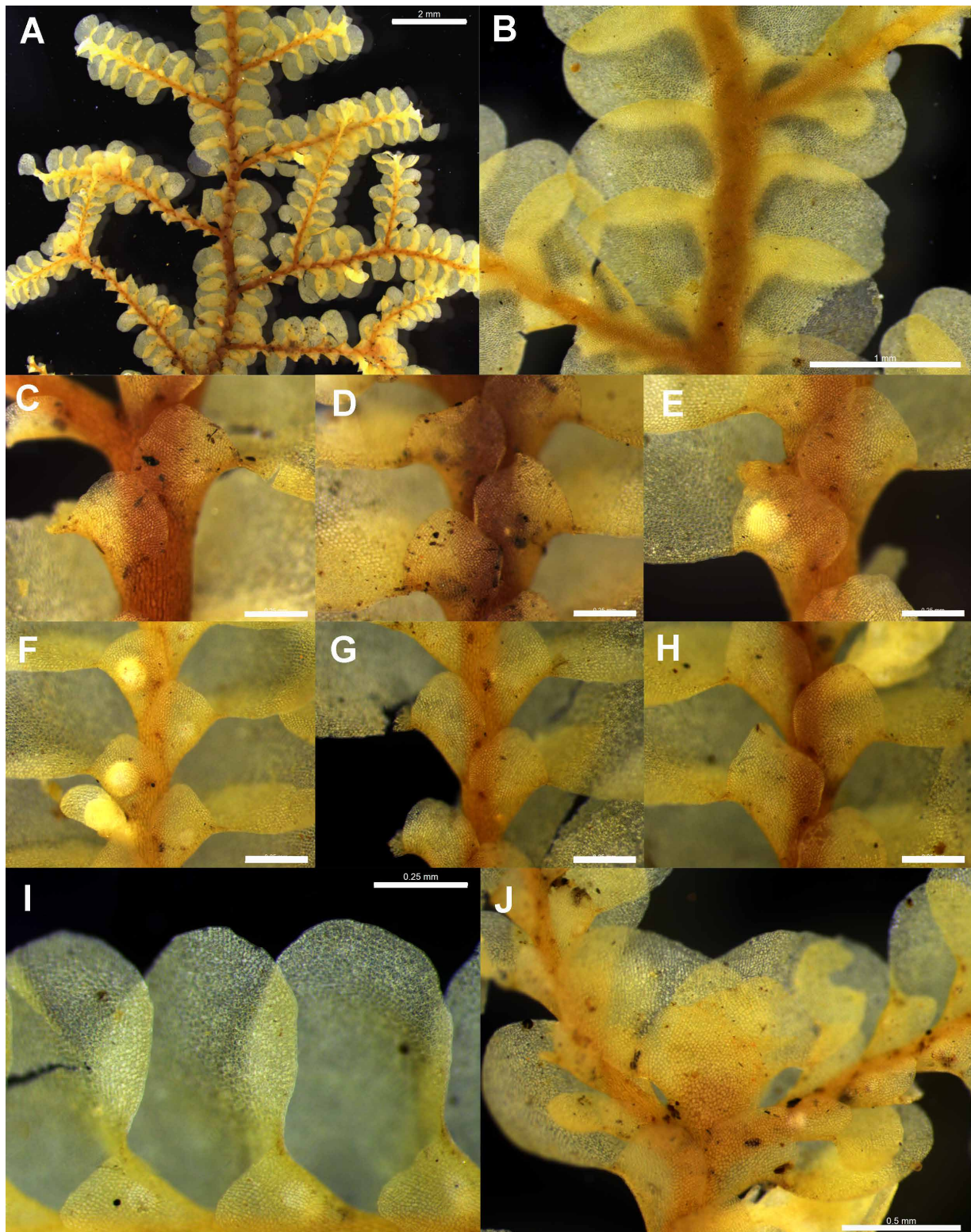


Fig. 15. *Radula javanica cordiloba* morph Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 µm). C-E: Primary shoot lobules (250 µm). F-H: Secondary shoot lobules (250 µm). I: Secondary shoot lobe margins (250 µm). J: Female bracts (500 µm). All from NSW974490.



Fig. 16. *Radula javanica cordiloba* morph Plate B. A: Ventral view of perianth (1 mm). B: Transverse section of primary stem (50 µm). C: Leaf-lobe margin (50 µm). D: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). All from NSW974490.

R. multiflora var. *reflexilobula* (MUCV6798). I had identified a number of *R. javanica* specimens as this variety, including several included in the phylogeny, all of which group within the *R. javanica* clade. I reported *R. multiflora* for the Chatham Islands east of New Zealand, also on specimens of *R. javanica* (Renner and de Lange 2009). I even described a subspecies of *R. cordiloba* from New Zealand, which is also based on *R. javanica* (Renner 2005), and last year went as far as elevating this to species rank (Renner et al. 2013b). Lobule characters were also the basis on which I conferred a Fijian specimen of *R. javanica* to *Radula reflexa*, in the molecular phylogeny of Devos et al. (2011 a, b). Similarly So's (2006) report of *R. reflexa* for Fiji was based on *R. javanica*. This species really is a lesson in humility.

Nomenclature: Six collections were cited in the protologue of *R. javanica*.

1. Java insula ad Sadjra Prov. Bantam (*Blume*)
2. Insula Mauritii (*Sieber*)
3. Nilgherries (*Mont.*)
- 4, 5. Owaihi et Ceylon Insulis (*Hb. Hk n. 51. 56*)
6. Insulis Carolinis, Ualan et Strong (*Lesson* in *Hb. Kunth. et Bongard*, *Mertens* in *Hb. Acad. Petrop.*).

Castle pointed out that Gottsche equated the island name 'Ualan' (= Kusiae Island) with the name of a collector. The specimen was collected by Strong on Ualan Island, and communicated to R.P. Pesson, then to Hb. Gottsche, to Hb. Bescherelle etc (Castle 1966).

In lectotypifying *R. javanica* on the Caroline Island specimen Castle (1966) stated 'The original description of *Radula javanica* Gottsche was based primarily on material that had been collected by Blume in Java and that had been cited in the *Hepaticae Javanicae* of Reinwardt, Blume and Nees under the name *R. boryana* N. ab E., in 1825' (Castle 1966 p. 74). The specimen collected by Blume in Bantam Province of Java is the first specimen cited by Gottsche et al. (1844). According to Castle, Gottsche (1861) pointed out that the collection upon which he based *R. javanica* contained two varieties which he designated 'variety *alpha originalis*', and

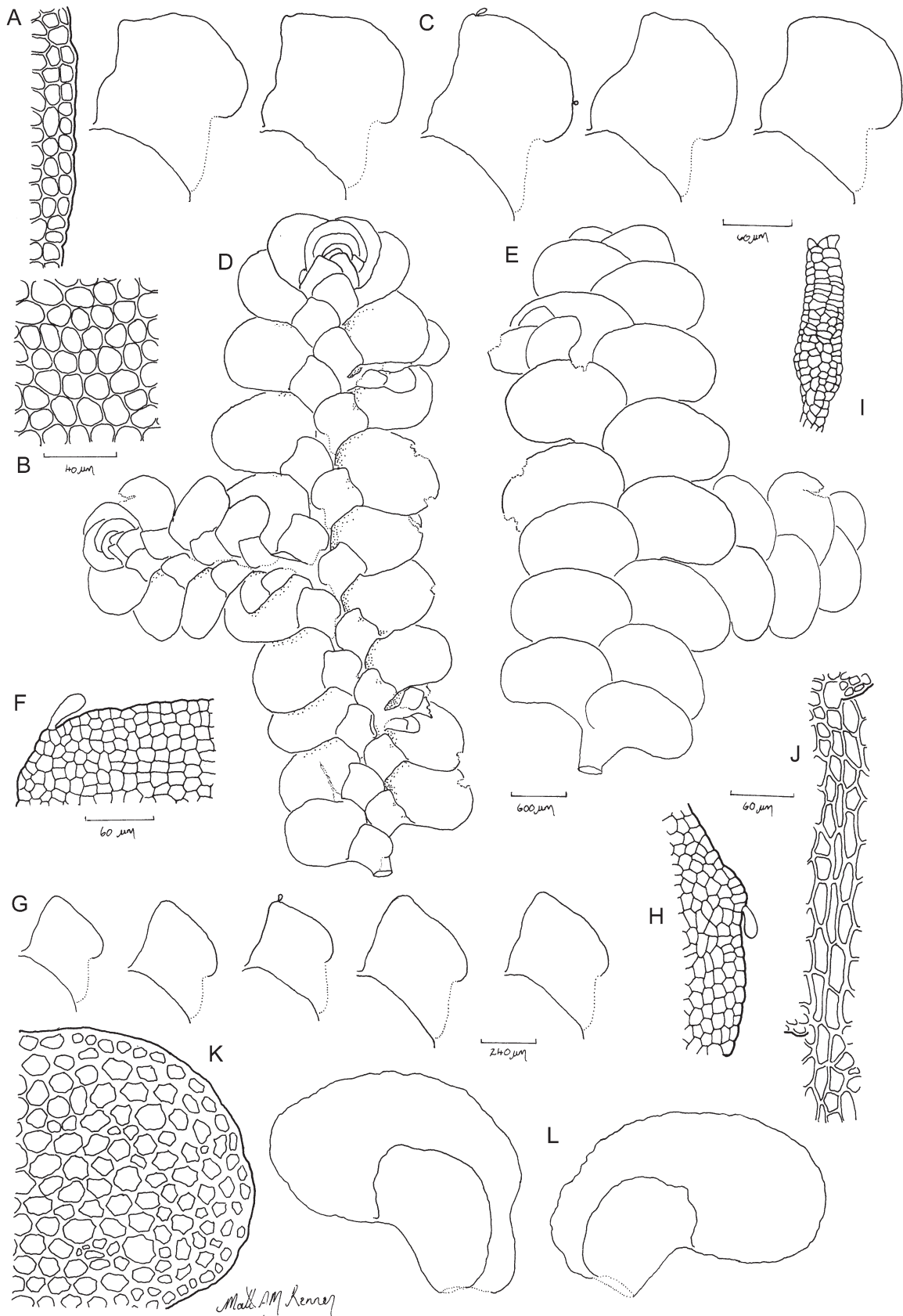


Fig. 17. *Radula javanica* cordiloba morph Line drawings. A: Lobe marginal cells. B: Lobe medial cells. C: Five lobules from primary shoots. D: Ventral view of primary shoot. E: Dorsal view of primary shoot. F: Lobule apex. G: Five lobules from secondary branches. H: Lobule interior margin. I: Archegonium. J: Cells on dorsal stem surface. K: Transverse stem section. L: Separated pair of female bracts. All from NSW974490.

‘variety *beta commutata*’. Gottsche associated with *alpha originalis* the Bantam collection in Herb. Blume from Java, and stated that it was conspecific with *Radula campanigera* Mont. Castle (1966) concurred with this assessment. Under variety *beta commutata* Gottsche cited the Lesson collection from the Caroline Islands as the first specimen. Castle claims that it is ‘consistent with nomenclatorial rules to retain the name *Radula javanica* Gottsche with *R. javanica* var *beta commutata* as its synonym and to designate the Caroline Islands collection as the lectotype’ (Castle 1966 p. 74). At any rate the six syntypes comprise maybe five different species.

Specimens examined: VANUATU: Sanma, E of Penaraou, S of Logmoli airstrip, Espiritu Santo, 14° 21'49" S, 166° 32'53" E, 600 m, Nov 2006, E.A. Brown s.n. (NSW974482, 974490).

AUSTRALIA QUEENSLAND: COOK: track from Big Tableland to O’Keefe Creek, 26 km S of Cooktown, 15° 43' S 145° 15' E, 400 m, 11 Dec 1990, J.A. Curnow 3969 (BRI-AQ807552; CANB9500753); J.A. Curnow 3961 (BRI-AQ807555; CANB9500745); Home Rule Falls, Wallaby Creek, 30 km SSE of Cooktown, 15° 44' S 145° 18' E, 240 m, 19 Oct 1995, H. Streimann 56997 (CANB9519063); Cape Tribulation north of Mossman, 30 June 1983, M.L. Hicks 11506 (BRI-AQ722900, as *Radula reflexa*); Daintree National Park: Between Thornton Beach and Noah Creek, 16° 09' 04" S, 145° 26' 28" E, 5 m, 25 Mar 2012, M.A.M. Renner 6329, V.C. Linis & E.A. Brown (NSW896726); M.A.M. Renner 6328b, V.C. Linis, E.A. Brown (NSW896725); The Daintree, tributary of Buchanan Creek, 16° 14' 33" S, 145° 25' 41" E, 135 m, 26 Mar 2012, M.A.M. Renner 6333, V.C. Linis & E.A. Brown (NSW896734); Mossman Gorge, near start of Circuit Track, 16° 28' S 145° 21' E, 4 June 1992, E.A. Brown 92/79, A.N.L. Doust & B.J. Conn (NSW295623); Rex Creek, 16° 28' S 145° 19' E, 10 Jul 2005, M.A.M. Renner 2034 & E.A. Brown (NSW872743); 16° 28' S 145° 19' E, 10 Jul 2005, M.A.M. Renner 2041 & E.A. Brown (NSW872741); Daintree National Park, Mossman Gorge, Rex Creek, 16° 28' 11" S, 145° 19' 37" E, 105 m, 24 Mar 2012, M.A.M. Renner 6298, V.C. Linis & E.A. Brown (NSW896687); upstream from swing-bridge, 16° 28' 13" S, 145° 19' 42" E, 105 m, 24 Mar 2012, M.A.M. Renner 6271, V.C. Linis & E.A. Brown (NSW896416); above intersection with Rex Loop track, 16° 28' 19" S, 145° 19' 32" E, 10 Jul 2005, M.A.M. Renner 2034 & E.A. Brown (NSW872743); Wurrumbu Stream, 16° 28' 02" S, 145° 19' 18" E, 150 m, 24 Mar 2012, M.A.M. Renner 6317, V.C. Linis & E.A. Brown (NSW896712); Mt. Lewis, SW of Mossman, 29 August 1982, M.L. Hicks 11173 (BRI-AQ722878, as *R. multiflora*); Mulgrave River, 17° 10' S 145° 52' E, without date, F.M. Bailey 607 (MEL1037793, as *R. acutiloba*); Freshwater Creek, Cairns, 1889, F.M. Bailey ex herb. F.M. Bailey 647 (BRI-AQ722868); Granite Creek, Bellenden Ker Expedition, 1889, F.M. Bailey, ex herb. F.M. Bailey 678 (BRI-AQ722869, as *R. javanica*); Mulgrave, 1889, F.M. Bailey ex herb. F.M. Bailey 607 (BRI-AQ332134); Smithfield, 2 July 1890, (?).C.J. Wild ex herb. C.J. Wild (BRI-AQ722870, 722871); North Queensland, Smithfield, Jul 1890, C.J. Wild ex herb. C.J. Wild (BRI-AQ539634); Wooroonooran National Park: Tributary of Babinda Stream, 30 m above junction with Babinda Stream., 17° 19' 59" S, 145° 51' 40" E, 85 m, 3 Apr 2012, M.A.M. Renner 6509, V.C. Linis & E.A. Brown (NSW909504); South Johnston River, McMillan Creek catchment, Gorrell Track c. 2 km S of South Johnston River picnic area (old forestry camp), 17° 40' 19" S, 145° 43' 38" E, 600 m, 6 Apr 2012, M.A.M. Renner 6564, V.C. Linis & E.A. Brown (NSW970435); South Johnston River catchment, Maple Creek, where crossed by Maple Creek Road, 17° 41' 18" S, 145° 41' 55" E, 590 m, 5 Apr 2012, M.A.M. Renner 6546, V.C. Linis & E.A. Brown (NSW978121); Waraker Creek, Cooroo Lands Road, 12 km W of Innisfail, 17° 32' S 145° 55' E, 80 m, 28 Jun 1984, H. Streimann 30034 (CANB84083890); Palmerston National Park: track to Tchupala Falls, 17° 36' S 145° 46' E, 11 July 1994, E.A. Brown 94/441, R.G. Coveny & B.C. Tan (NSW297008); 17° 36' S 145° 47' E, 2 Jul 1984, W.B. Schofield 80336 & M.I. Schofield (NSW734519); NORTH KENNEDY: Rockingham Bay, Nord Ost Australia, without date, J. Dallachy s.n. (MEL1037774 p.p.); Cardwell, Dalrymple Creek track, 1 Sep 1985, G.A.M. Scott s.n. (MUCV6798 as *R. multiflora* var. *reflexilobula*); BURKE: Banks of Campbells Creek, 18° 10' S 141° 18' E, 14 June 1944, H. Flecker s.n. (MEL1037775); DARLING DOWNS: Mt Tyson, 27° 34' S 151° 33' E, 16 February 1939, H. Flecker s.n. (MEL1037819); NEW SOUTH WALES: NORTH COAST: below Marshall’s Falls, Richmond River, 28° 51' S 153° 27' E, Aug 1902, W.W. Watts 546 (NSW764151).

NEW ZEALAND: KERMADEC ISLANDS: Raoul Island, Denham Bay Track, above Orange Cove, 29° 14' 56" S 177° 55' 54" W, 208 m, 18 May 2011, P.J. de Lange K742 (AK325678); Raoul Island, Moumoukai Track, 29° 16' 0" S 177° 54' 0" W, 384 m, 8 May 2009, P.J. de Lange K224 & D.C. Havell (AK313206); 336 m, 15 May 2011, P.J. de Lange K741 (AK325676); Raoul Island, Denham Bay Track, 29° 15' 39" S 177° 56' 16" W, 271 m, 18 May 2011, P.J. de Lange K744 (AK325681); Raoul Island, 1956, R.C. Cooper 44350 (CHR558807); Sunshine Valley, below Sunshine Waterfall in ravine system, 29° 17' 11" S 177° 55' 46" W, 53 m, 15 May 2011, P.J. de Lange L735 (AK325646); CHATHAM ISLANDS: Rangiauria (Pitt Island), Flower Pot – Glory Road, Tupuangi Stream (upper tributary), 44° 14' S 176° 13' W, 10 m, 30 May 2008, P.J. de Lange CH1717 & P.B. Heenan (AK303450).

COOK ISLANDS: RAROTONGA: Maungatea Bluff Track, ‘The Pinnacle’, 21° 13' 0" S 159° 49' 0" W, 300 m, 6 Jul 2010, P. J. de Lange CK191 & T.J. Martin (AK323599); Te Maunga Track, upper Tupapa Stream, 21° 13' 0" S 159° 45' 0" W, 220 m, 8 Jul 2010, P. J. de Lange CK178 & T.J. Martin (AK322720); Maungatea Bluff Track, ‘The Pinnacle’, 21°13' 0" S 159°49' 0"W, 300 m, 6 Jul 2010, P. J. de Lange CK193 & T.J. Martin (AK323601).

FJI: VITI LEVU: Southern sector of Namosi Road, c. 2 km from turnoff to village, 18° 03' 24" S, 178° 09' 27" E, 330 m, 31 Aug 2011, M.A.M. Renner 5387 (CANB, F, NSW889458, SUVA); West of Namosi Village, 18° 03' 03" S, 178° 07' 09" E, 130 m, 30 Aug 2011, L. Söderström 2011/057, M. von Konrat et al. (NSW978129); Rairaimatuku Plateau, Monasavu, on road to Tominiivi, 17° 43' 30" S, 178° 02' 15" E, c. 900 m, 4 Sep 2011, M.A.M. Renner 5577 (F, NSW895228, SUVA).

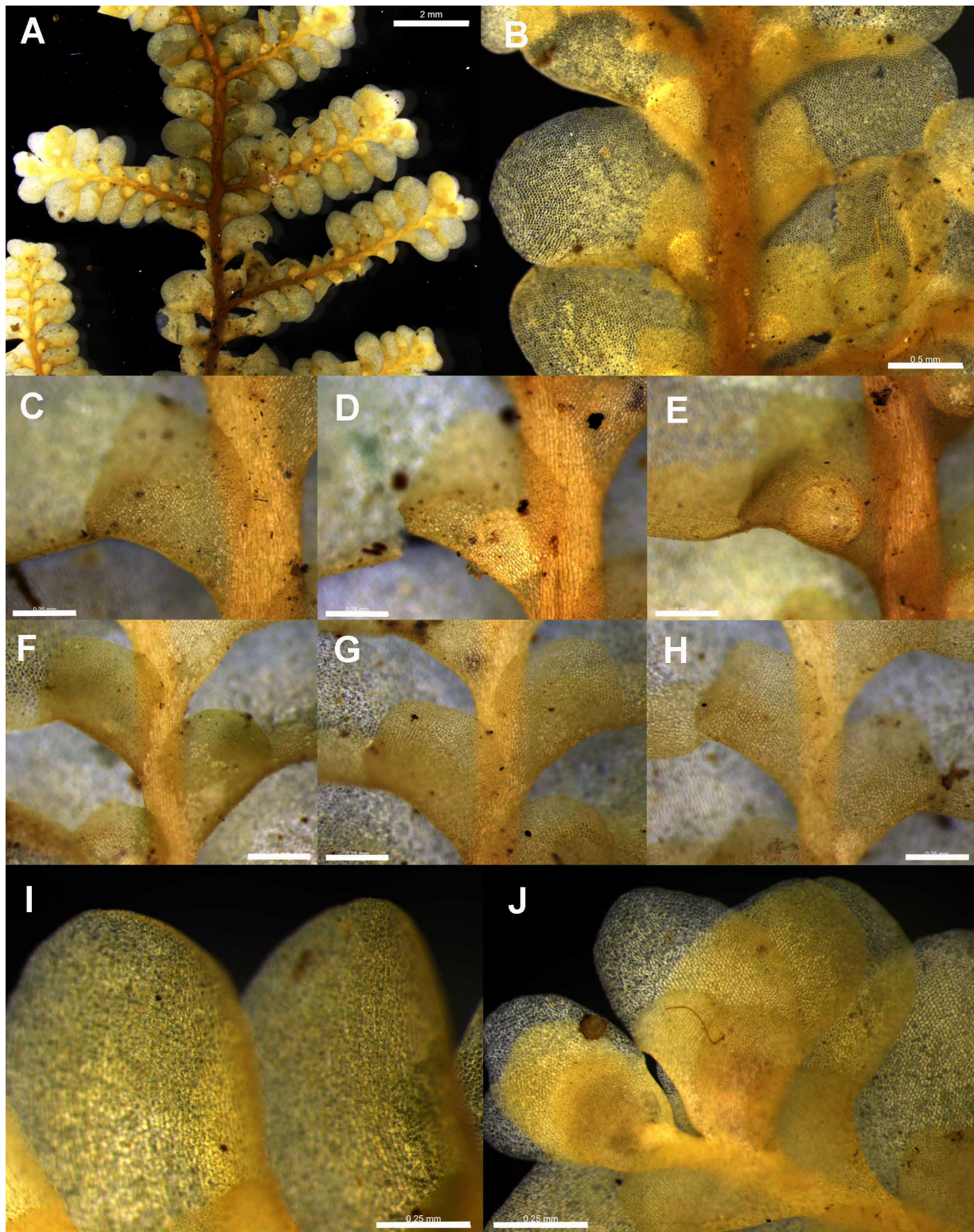


Fig. 18. *Radula* sp. (n) Moa Island CANB9500180 Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 µm). C-E: Primary shoot lobules (250 µm). F-H: Secondary shoot lobules (250 µm). I: Secondary shoot lobe margins (250 µm). J: Female bracts (500 µm). All from CANB9500180.

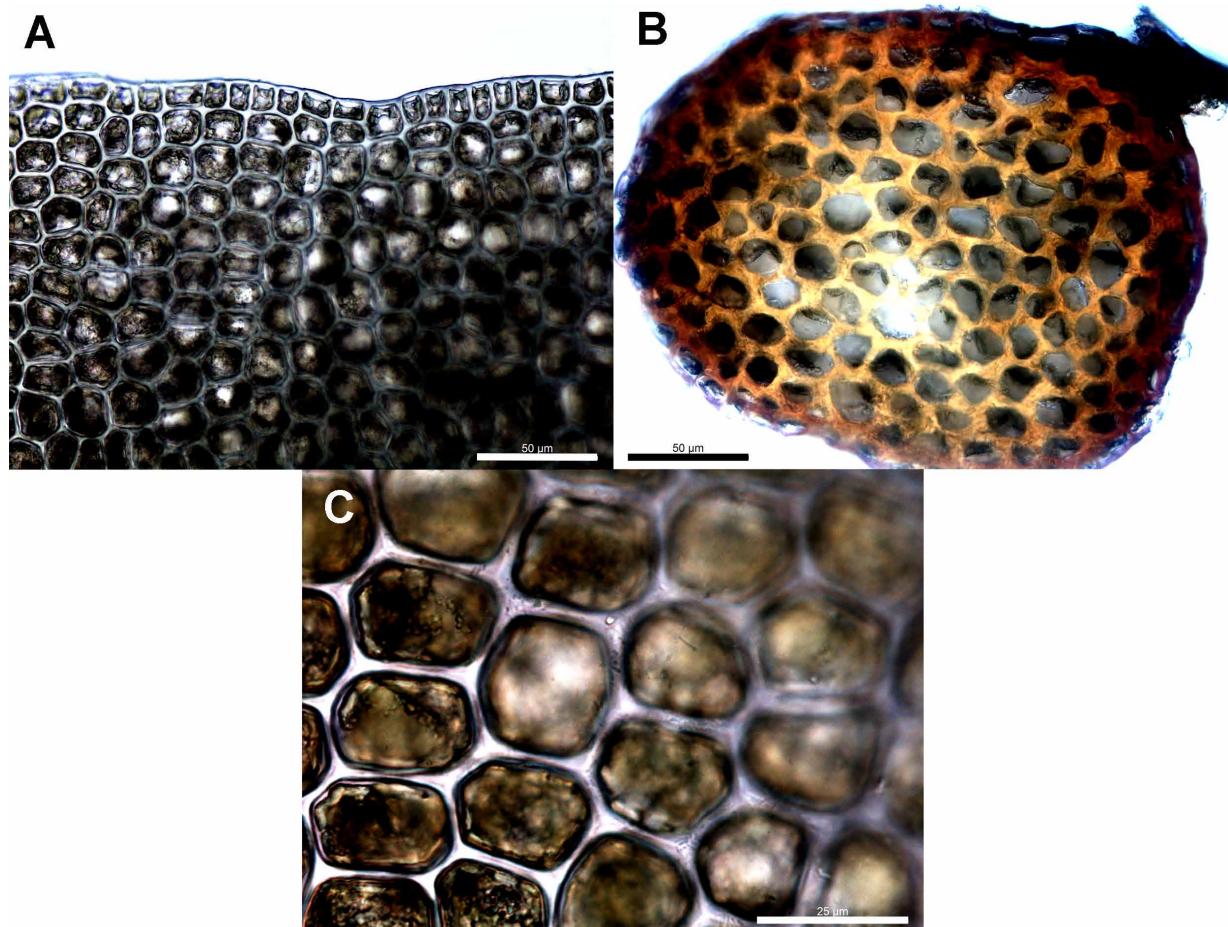


Fig. 19. *Radula* sp. (n) Moa Island (CANB9500180) Plate B. A: Leaf-lobe margin (50 µm). B: Transverse section of primary stem (50 µm). C: Leaf-lobe medial cell surface, showing absence of ornamentation (25 µm). All from CANB9500180.

SAMOA: without date, *Reinecke 79 ex herb Steph.* (G); *Reinecke 81 ex herb Steph.* (G); *Reinecke s.n. ex herb Steph.* (G).

Misidentified specimens: SOUTH AMERICA: BOLIVIA: Cochabamba, Chapare, Parque Machia, cerca Villa Tunari, 16° 58' S 65° 24' W, 240 m, 31 Oct 2002, S. Churchill, M. Decker & F. Mogro 22187 (MO5647947), det *R. javanica* is an undetermined species of subg. *Radula*, it is not *R. javanica*; Tarija, Arce, Municipio de Padcaya, Canton Emborozu, Reserva Natural Alarachi. Zona Coyatal, Rio Emborozu Chic, 22° 14' 18" S 64° 34' 19" W, 1220 m, 21 Sep 2004, S. Churchill, M. Serrano et al. 23450 (MO5632134), det *R. javanica* is *R. episcia* Spruce which is a member of subg. *Volutoradula*.

***Radula* sp. Moa Island (CANB9500187)**

Description [from CANB9500187]: Forming loose wefts of pendant-procumbent shoots, glaucous and brown in herbaria. Shoot systems dimorphic, pinnately branched, with additional pseudodichotomous branching due to production of pairs of subfloral innovations below gynoecia, primary shoots 2400–3000 mm wide and up to 80 mm long. Older shoot sectors retaining leaf-lobes. Stems 200–300 µm diameter, with cortical cells in a single tier of 50–70 rows, cell walls yellow-brown to brown pigmented, external free cortical cell wall unthickened, radial longitudinal cortical walls unthickened or with continuous thickening, inner tangential walls continuously thickened by confluent bulging trigones; medullary cells in c. 150 rows, cell walls yellow pigmented, cell with large bulging trigones, usually confluent across cell walls. Cortical cells on dorsal stem surface arranged in straight longitudinal rows on young and mature shoot sectors. Leaf insertion exceeding dorsal stem mid-line, overlapping across one to three dorsal cortical cells. Leaf insertion not attaining the ventral stem mid-line, leaving one to three ventral cortical cell rows leaf-free. Leaf lobes oblong-elliptic, 1100–1700 µm long by 860–1300 µm wide on primary shoots, 1000–1250 µm long by 540–880 µm wide on secondary shoots, imbricate, not falcate, acroscopic base not sharply deflexed away from stem, concave, outer portion not rolled downward or forward, partially to completely interlocking over the dorsal stem surface, stem

partially visible between leaf lobes in dorsal view or not; margins minutely denticulate due to bulging marginal cells, the interior lobe margin weakly ampliate, usually reaching the opposite stem margin, dorsal margin straight to shallowly curved, ventral margin straight, interior and exterior margins curved; angle between postical lobe margin and keel 45–60°. Lobules rhombic-ovate, remote to contiguous, plane, one eighth to one sixth the lobe area, 740–1060 µm long by 520–750 µm wide on primary shoots, 540–640 µm long by 340–480 µm wide on primary shoots, keel straight to weakly arched, angle between keel and stem 135°, keel turning through 45–90° at keel-lobe junction, keel apex and postical lobe margin shallowly notched; interior lobule margin free for one half to two thirds its length, free portion weakly ampliate, not adpressed against the stem, sometimes reaching the opposite stem margin and partially concealing the stem in ventral view; acroscopic margin curved, apical portion inclined inward toward the stem; apex rounded, free exterior margin straight to shallowly curved, plane, margins irregular, and may be crenulated due to bulging marginal cells. Lobe-lobule junction level with the acroscopic end of stem insertion. Lobule apex bearing a single papilla, with two papilla situated on the interior lobule margin above the stem insertion. Leaf lobe cells rounded or hexagonal, arranged in loose rows, uniformly sized, 17–30 µm long by 17–21 µm wide, thin walled with concave trigones, medial wall thickenings absent. Cells of lobe margin smaller than those of leaf middle, quadrate, exterior and interior cell walls not differentially evenly thickened. Leaf lobe cell surface smooth. Oil-bodies not known. Asexual reproduction absent. Dioicous. Androecia not known. Gynoecia terminal on branch shoots, subtended by one or two subfloral innovations that are the same size as the branch shoot and are again fertile. Archegonia c. 200 µm tall, archegonia neck seven or eight cell columns, c. 25 per gynoecium on a small disc of tissue, encompassed by the protoperianth. Female bracts in one pair, subsymmetrical, imbricate, elliptic-oblong, lobe 1400–1600 µm long by 800–1100 µm wide, margins minutely crenulate; lobules ovate to elliptic oblong, one third to one quarter the lobe area, apex rounded, keel straight to arched, margins crenulate; bract insertion lines interlocking dorsally and ventrally, insertion equitant. Perianths and sporophytes not known.

Figs 18–20.

Specimens examined: AUSTRALIA: QUEENSLAND: COOK: Northern end of Moa Island, Moa Peak, 10°10'S 142°16'E, 370 m, 11 Feb 1989, *D.L. Jones 89-10* (CANB9500187); *D.L. Jones 89-3* (CANB9500180).

Distribution and habitats: In Australia known from a single collection from Moa Island in the Torres Strait. Here, *R. sp.* (n) 'Moa Island CANB9500187' grew as an epiphyte on tree trunks in tall monsoon rainforest at 370 m. The species is probably more widespread along either side of the Torres Strait.

Identification: Distinctive in its pinnately branched shoot systems, elliptic lobules, and smooth leaf-lobe cell surfaces.

Remarks: This specimen was identified as *R. buccinifera* (Hook.f. & Taylor) Gottsche, Lindenb. et Nees. While it is not allied to that species, I have been unable to establish its identity.

Species excluded from the Australasian flora

Radula kurzii Steph. *Hedwigia* 23: 153. 1884

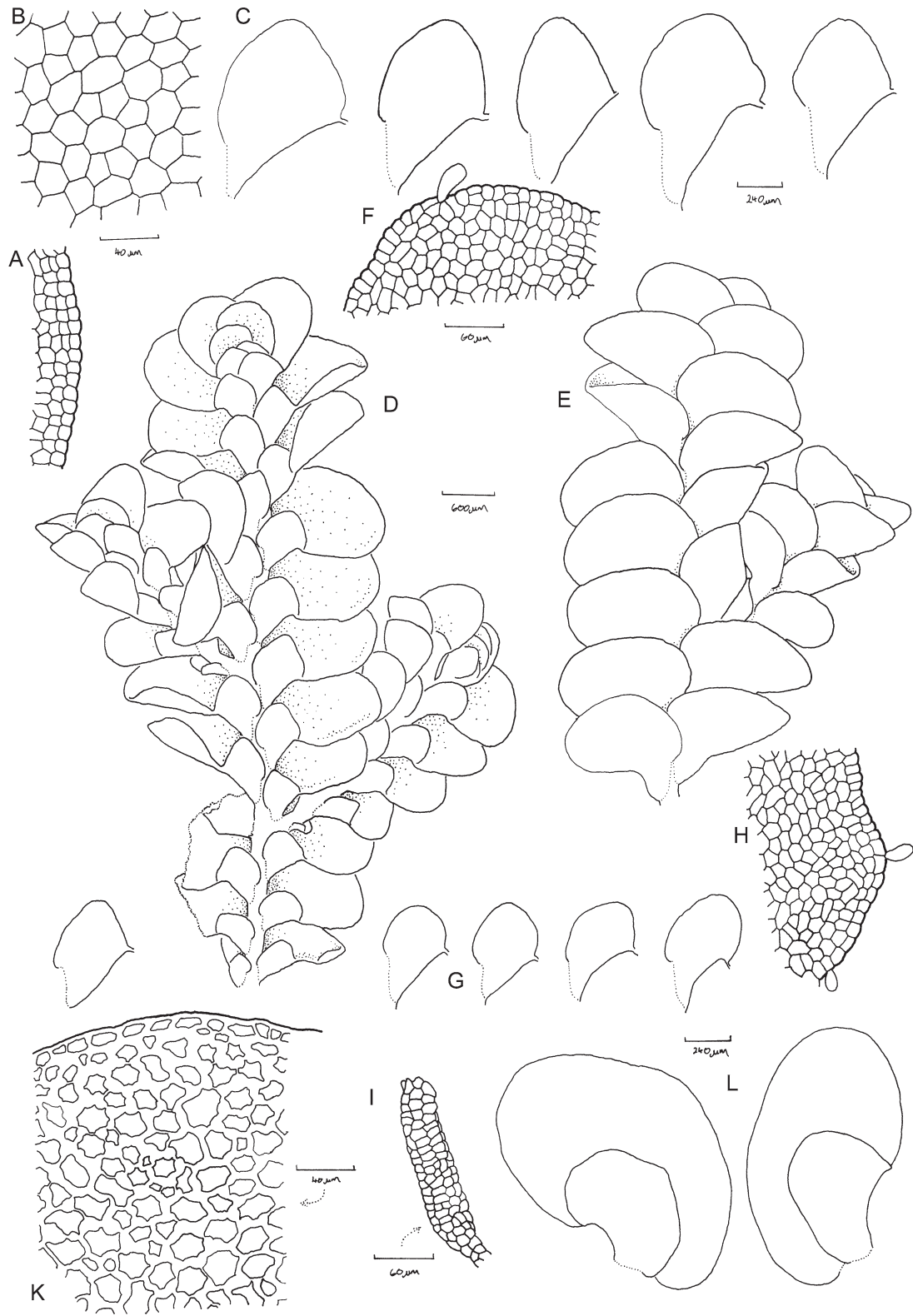
Type: Hab. South Andaman. leg. Kurz (Hb. Gottsche)

Radula kurzii was recorded by Yamada (1984) from several specimens collected on rock in the Wet Tropics Bioregion, including Mt Lewis and Mt Bartle Frere by M.L. Hicks. I have seen one of these collections (*Hicks 10901*) and it is *Radula loriana* Castle, and I assume the other collections made from similar sites in the same region are also referable to *R. loriana*, which is common in rainforests from close to sea level to around 1500 m. Although I have not seen the type of *R. kurzii*, a type specimen of one of its synonyms, *R. speciosa* Gottsche (BM000969285!) has been seen, and nothing approaching this entity has been observed in Australia. Yamada's record of *R. kurzii* is probably based on misidentifications of the outwardly similar *R. loriana*, and should be excluded from the Australian flora. Stephani had earlier determined as *R. kurzii* a specimen from Norfolk Island, but did not publish this record. This specimen is also closer to *R. loriana*.

Misidentified specimens examined: AUSTRALIA: QUEENSLAND: COOK: over rock outcrop near Josephine Falls, north of Innisfail, 23 June 1982, *M.L. Hicks 10901* (BRI-AQ722876) is *R. loriana*. AUSTRALIA: NORFOLK ISLAND: *Isaac Robinson ex herb Steph.* (BM) is *R. loriana*.

Radula sharpii K.Yamada. *Journal of Japanese Botany* 60: 260. 1985

Type: Papua New Guinea: Morobe: Aseki-Mdamna Track, 1 km SW of Aseki, 1350 m, advanced secondary vegetation beside large stream in deep gorge, on *Ficus* trunk beside stream, 23 Jan 1981. *H. Streimann 12449* (holotype: CANB8109872! Isotypes: JE, LAE, NICH).



Made AM Renner.

Fig. 20. *Radula* sp. Moa Island (CANB9500180) Line drawings. A: Lobe marginal cells. B: Lobe medial cells. C: Five lobules from primary shoots. D: Ventral view of primary shoot. E: Dorsal view of primary shoot. F: Lobule apex. G: Five lobules from secondary branches. H: Lobule interior margin. I: Archegonium. K: Transverse stem section. L: Separated pair of female bracts. All from CANB9500180.

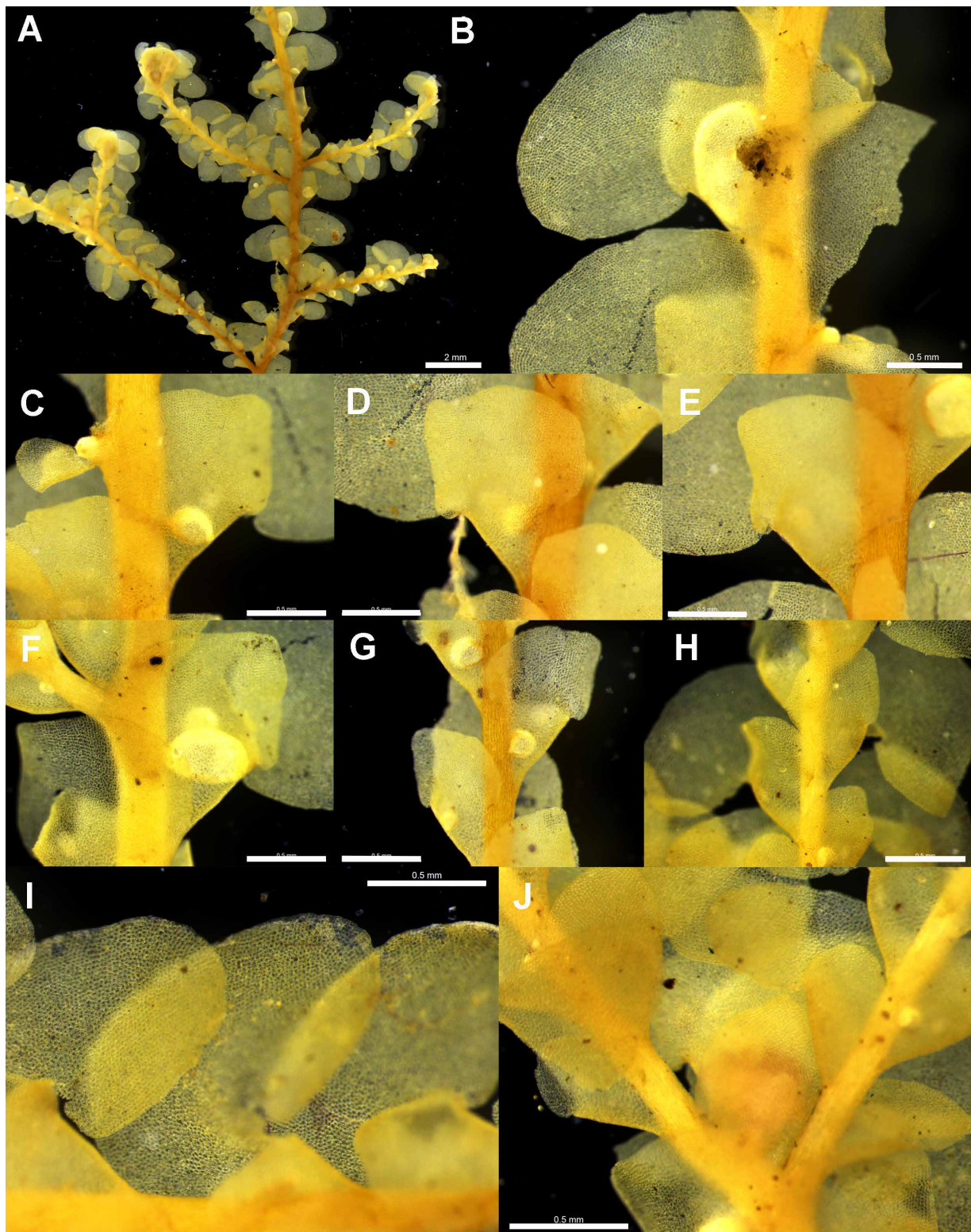


Fig. 21. *Radula sharpii* Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μ m). C-E: Primary shoot lobules (500 μ m). F-H: Secondary shoot lobules (500 μ m). I: Secondary shoot lobe margins (500 μ m). J: Female bracts (500 μ m). All from CANB8109872.

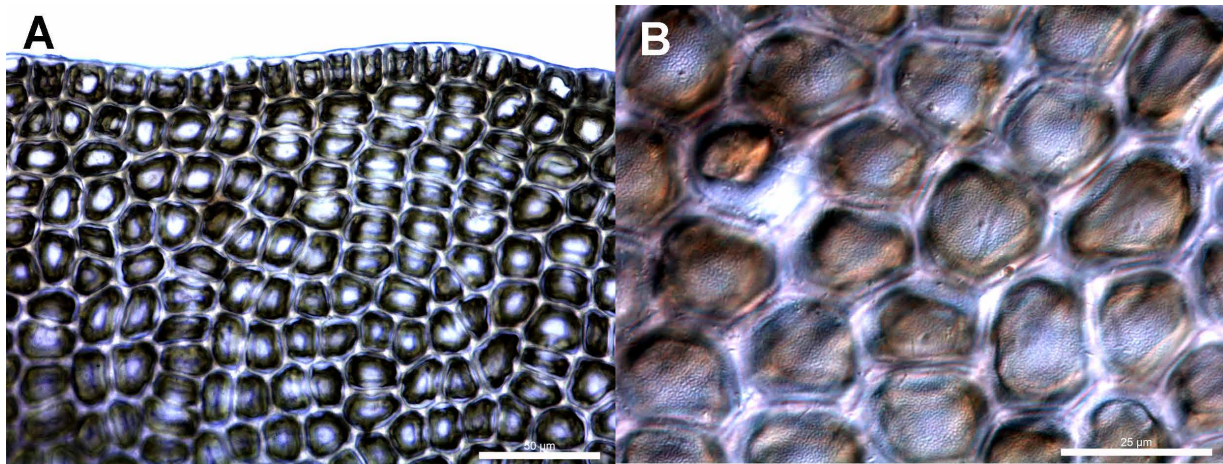


Fig. 22. *Radula sharpii* Plate B. A: Leaf-lobe margin (50 µm). B: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). Both from CANB8109872.

Fig. 21–22.

Described from Papua New Guinea, then recorded for Queensland by Yamada (1987), on the basis of a single collection from Mossman Gorge collected by Ilma Stone. Subsequent collections from the Wet Tropics have also been identified as *R. sharpii*, all are referable to *R. oreopsis*.

Specimens examined: PAPUA NEW GUINEA: MOROBE: Mount Missim Track, 10 km NNE of Wau, 7° 17' S 146° 47' E, 1380 m, 18 Aug 1982, *H. Streimann* 22954, (CANB8405062); Poyu Village, 1.5 km SE of Aseki, 7° 22' S 146° 11' E, 1300 m, 6 Dec 1982, *H. Streimann* 26152 (CANB9006045).

Representative misidentified specimens examined: AUSTRALIA: QUEENSLAND: COOK: Daintree National Park: Mossman Gorge, 28 Jun 1982, *I.G. Stone*, (MELU H-1256, MUCV6101 is *R. oreopsis*); Cardstone, Tully, 3 Sep 1985, *G.A.M. Scott* (MUCV6603 is *R. oreopsis*); creeks E. of Cochable Creek Causeway, Cardstone, Tully, 3 Sep 1985, *G.A.M. Scott*, MUCV6643 is *R. oreopsis*.

Radula multiflora Gottsche ex Steph.

Type: Papua New Guinea: New Ireland: Bismarck Archip., New Hannover Island, 20 Jul 1875, Gazelle Exped., *F. C. Neumann s.n.* as *R. javanica* G00282365 (15113)!

It is difficult to form an impression of *R. multiflora* from the type material, which comprises two fragmented and damaged branch shoots bearing numerous gynoecea.

The most distinctive thing about these is the lobules almost roundish, and free for up to two thirds their interior length, the free portion of which is weakly ampliate and overlies the stem. None of the lobule-reflexion supposedly characteristic of this species is apparent. Within the type specimen Yamada separated out a shoot that looks to me identical, and called it *R. vriesiana*. If Yamada is correct, *R. multiflora* must be lectotypified.

Australian material identified as *R. multiflora* generally agrees with *R. javanica*, except lobules on primary shoots have a broadly ampliate interior margin, and in this character are similar to *R. cordiloba*, except that the ampliation is even more pronounced. While the material does not seem to be a good match for *R. multiflora*, it is possible that it represents a species other than *R. javanica*, and I have over-looked the significance of the differences in lobule shape.

A specimen from Chatham Island (Renner and de Lange 2009) was attributed to this species on the basis of lobule shape and reflexion of the interior lobule margin. These characters are shared by many individuals resolved within the *R. javanica* clade by this study. The Chatham Island record of *R. multiflora* was based on a misidentification of *R. javanica*, and *R. multiflora* should also be excluded from the New Zealand flora.

Representative misidentified specimens examined: AUSTRALIA: QUEENSLAND: COOK: Mt Lewis, 16° 35' S 145° 17' E, 29 Aug 1982, *M.L. Hicks* 11173 (BRI-AQ722878 = *R. javanica*); Daintree National Park: Mossman, Rex Creek, 30 Jun 1982, *I.G. Stone s.n.* (MUCV6069 is *R. javanica*); Mossman Gorge, 27 May 1975, *I.G. Stone s.n.* (MUCV4653, as (provisionally)

R. portoricensis then *R. multiflora* = *R. javanica*); Mossman Gorge, G.A.M. Scott s.n. (MELU347 = *R. javanica*); NORTH KENNEDY: Tully, Cardstone, H-tree Creek, 20 May 1985, I.G. Stone s.n. (MUCV7229 = *R. javanica*); Cardwell, Dalrymple Creek track, on top, 1 Sep 1985, G.A.M. Scott s.n. (MUCV6817 = *R. mittenii*); Cardwell, Dalrymple Creek track, W. of top, 1 Sep 1985, G.A.M. Scott s.n. (MUCV6820 = *R. javanica*); Cardwell, Dalrymple Creek track, half way from watershed to creek, 1 Sep 1985, G.A.M. Scott s.n. (MUCV6822 = *R. javanica*).

NEW ZEALAND, CHATHAM ISLANDS: Rangiauria (Pitt Island), Flower Pot – Glory Road, Tupurangi Stream (upper tributary), 44° 14' S 176° 13' W, 10 m, 30 May 2008, P.J. de Lange CH1717 & P.B. Heenan (AK303450 = *R. javanica*).

Radula reflexa Nees et Mont. *Annales des Sciences Naturelles, Botanique*, sér. 2 19: 255. 1843

Type: Indonesia. Moluccas Is, Amboina, J. T. Labillardière, hb. Mont. Lectotype designated by Castle (1965): PC-35426, isolectotypes: BM! G00046053 (17202)! PC-35425, W-5449).

Radula reflexa differs from *R. decurrens* in the lobules being reflexed perpendicular to the stem, rather than at an angle to it. In *R. decurrens* the lines of reflexion form a zig-zag pattern across the stem. The lobules in *R. decurrens* exceed the opposite stem margin.

In Australia, many *Radula* with reflexed lobules have been attributed to *R. reflexa* on that basis. Australian records of *R. reflexa* are based on misidentifications of *R. javanica*, predominantly the rheophytic morph. The Fijian plants conferred to *R. reflexa* by myself in the molecular phylogeny of Devos et al. (2011a,b) are also *R. javanica*.

Representative misidentified specimen examined: AUSTRALIA: QUEENSLAND: COOK: Cape Tribulation north of Mossman, over rock outcrop in rainforest 30 Jun 1983, M.L. Hicks 11506 (BRI-AQ722900 = *R. javanica*); Fishers Falls, Mt Bellenden Ker, 11 Sep 1985, G.A.M. Scott s.n. (MUCV7428 = *R. javanica*); NORTH KENNEDY: H-tree Creek, Cardstone, Tully, 20 May 1985, I.G. Stone s.n. (MUCV7234 = *R. javanica* with *R. mittenii*); Dalrymple Creek track, Cardwell, 1 Sep 1985, G.A.M. Scott s.n. (MUCV6840 = *R. javanica*); Mt Mackay State Forest, W of Tully, 29 Jul 1984, M. Thorsborne & I.G. Stone s.n. (MUCV5888 = *R. mittenii*).

Table 3. Voucher details and GenBank accession numbers for sequences. All KM numbers were newly generated for this study.

Voucher number	Taxon	Collector	Coll. no.	atpB-rbL	trnG	trnL-F
NSW896401	<i>Radula acutiloba</i>	M.A.M. Renner	6262	KM220233	KM220096	KM220164
NSW976716	<i>Radula acutiloba</i>	M.A.M. Renner	5889	KM220231	KM220094	KM220162
NSW978099	<i>Radula acutiloba</i>	M.A.M. Renner	5890	KM220232	KM220095	KM220163
NSW978127	<i>Radula decurrens</i>	L. Söderström	2011/056	KM220197	KM220062	KM220127
NSW872743	<i>Radula javanica</i>	M.A.M. Renner	2034	KM220205	KM220070	KM220135
NSW889458	<i>Radula javanica</i>	M.A.M. Renner	5387	KM220203	KM220068	KM220133
NSW896416	<i>Radula javanica</i>	M.A.M. Renner	6271	KM220199	KM220064	KM220129
NSW896677	<i>Radula javanica</i>	M.A.M. Renner	6291	KM220193	KM220058	KM220123
NSW896683	<i>Radula javanica</i>	M.A.M. Renner	6294	KM220194	KM220059	KM220124
NSW896687	<i>Radula javanica</i>	M.A.M. Renner	6298	KM220180	KM220049	KM220110
NSW896689	<i>Radula javanica</i>	M.A.M. Renner	6300	KM220204	KM220069	KM220134
NSW896712	<i>Radula javanica</i>	M.A.M. Renner	6317	KM220217	KM220081	KM220148
NSW896725	<i>Radula javanica</i>	M.A.M. Renner	6328 b	KM220198	KM220063	KM220128
NSW896726	<i>Radula javanica</i>	M.A.M. Renner	6329	KM220201	KM220066	KM220131
NSW896734	<i>Radula javanica</i>	M.A.M. Renner	6333	KM220182	KM220050	KM220112
NSW904735	<i>Radula javanica</i>	P.J. de Lange	K224	KM220190	KM220056	KM220120
NSW905125	<i>Radula javanica</i>	P.J. de Lange	K741	KM220169	KM220037	KM220099
NSW905502	<i>Radula javanica</i>	P.J. de Lange	K742	KM220170	KM220038	KM220100
NSW909504	<i>Radula javanica</i>	M.A.M. Renner	6509	KM220195	KM220060	KM220125
NSW970435	<i>Radula javanica</i>	M.A.M. Renner	6564	KM220183	-----	KM220113
NSW974482	<i>Radula javanica</i>	E.A. Brown	s.n.	KM220224	KM220088	KM220155
NSW974490	<i>Radula javanica</i>	E.A. Brown	s.n.	KM220222	KM220086	KM220153
NSW978121	<i>Radula javanica</i>	M.A.M. Renner	6546	KM220218	KM220082	KM220149
NSW978129	<i>Radula javanica</i>	L. Söderström	2011/057	KM220219	KM220083	KM220150
NSW978175	<i>Radula javanica</i>	M.A.M. Renner	5045	KM220185	KM220051	KM220115
AK322720	<i>Radula javanica</i>	P.J. de Lange		KM220208	KM220072	KM220138
AK323599	<i>Radula javanica</i>	P.J. de Lange		KM220207	KM220071	KM220137
AK323601	<i>Radula javanica</i>	P.J. de Lange		KM220206	-----	KM220136
NSW974452	<i>Radula javanica</i>	M.A.M. Renner	5505	KM220212	KM220076	KM220143
NSW896665	<i>Radula mittenii</i>	M.A.M. Renner	6282	KF432308	KF432394	KF440476
NSW896672	<i>Radula mittenii</i>	M.A.M. Renner	6288	KF432303	KF432389	KF440471

Voucher number	Taxon	Collector	Coll. no.	atpB-rbcl	trnG	trnL-F
NSW896685	<i>Radula mittenii</i>	M.A.M. Renner	6296	KF432304	KF432390	KF440472
NSW897201	<i>Radula mittenii</i>	M.A.M. Renner	6486	KF432305	KF432391	KF440473
NSW897206	<i>Radula mittenii</i>	M.A.M. Renner	6489	KF432302	KF432388	KF440470
NSW909503	<i>Radula mittenii</i>	M.A.M. Renner	6508	KM220172	KM220040	KM220102
NSW909664	<i>Radula mittenii</i>	M.A.M. Renner	6497	KF432306	KF432392	KF440474
NSW889291	<i>Radula oceania</i>	M.A.M. Renner	5322	KM220191	KM220057	KM220121
NSW889321	<i>Radula oceania</i>	M.A.M. Renner	5332	KM220187	KM220053	KM220117
NSW889374	<i>Radula oceania</i>	M.A.M. Renner	5358	KM220166	KM220034	-----
NSW889376	<i>Radula oceania</i>	M.A.M. Renner	5359 a	KM220188	KM220054	KM220118
NSW895198	<i>Radula oceania</i>	M.A.M. Renner	5571	KM220196	KM220061	KM220126
NSW895229	<i>Radula oceania</i>	M.A.M. Renner	5578	KM220186	KM220052	KM220116
NSW974315	<i>Radula oceania</i>	M.A.M. Renner	5732	KM220215	KM220079	KM220146
NSW978101	<i>Radula oceania</i>	M.A.M. Renner	5717	KM220181	-----	KM220111
NSW889516_1	<i>Radula oceania</i>	M.A.M. Renner	5412	KM220165	KM220033	KM220096
NSW889516_2	<i>Radula oceania</i>	M.A.M. Renner	5412	KM220192	-----	KM220122
NSW974316	<i>Radula oceania</i>	M.A.M. Renner	5741	KM220216	KM220080	KM220147
NSW896415	<i>Radula oreopsis</i>	M.A.M. Renner	6270	KM220175	KM220043	KM220105
NSW896659	<i>Radula oreopsis</i>	M.A.M. Renner	6278	KM220200	KM220065	KM220130
NSW896681	<i>Radula oreopsis</i>	M.A.M. Renner	6292	KM220176	KM220044	KM220106
NSW896698	<i>Radula oreopsis</i>	M.A.M. Renner	6309	KM220171	KM220039	KM220101
NSW899756	<i>Radula oreopsis</i>	M.A.M. Renner	6543	KM220177	KM220046	KM220107
NSW970425	<i>Radula oreopsis</i>	M.A.M. Renner	6572	KM220178	KM220047	KM220108
NSW970428	<i>Radula oreopsis</i>	M.A.M. Renner	6574	KM220173	KM220041	KM220103
NSW978100	<i>Radula oreopsis</i>	M.A.M. Renner	6551	KM220179	KM220048	KM220109
NSW970377	<i>Radula oreopsis</i>	M.A.M. Renner	6581	KM220174	KM220042	KM220104
NSW889416	<i>Radula sp.</i>	M.A.M. Renner	5373	KM220230	KM220093	KM220161
NSW850519	<i>Radula sp.</i>	C.D. Kilgour	952	-----	-----	KM220140
NSW895228	<i>Radula sp.</i> NSW895234	M.A.M. Renner	5577	KM220211	KM220075	KM220142
NSW895234	<i>Radula sp.</i> NSW895234	M.A.M. Renner	5583	KM220210	KM220074	KM220141
NSW895644	<i>Radula sp.</i> NSW973452	M.A.M. Renner	5767	KM220189	KM220055	KM220119
NSW973452	<i>Radula sp.</i> NSW973452	M.A.M. Renner	5732	KM220202	KM220067	KM220132
NSW978103	<i>Radula sp.</i> NSW973452	M.A.M. Renner	5782	KM220167	KM220035	KM220097
NSW974317	<i>Radula sp.</i> NSW974317	M.A.M. Renner	5717	KM220214	KM220078	KM220145
NSW978178	<i>Radula sp.</i> NSW974317	M.A.M. Renner	5691	KM220184	-----	KM220114
NSW890202	<i>Radula sp.</i> NSW974474	M.A.M. Renner	5522	KM220168	KM220036	KM220098
NSW895197	<i>Radula sp.</i> NSW974474	M.A.M. Renner	5570	KM220213	KM220077	KM220144
NSW974472	<i>Radula sp.</i> NSW974474	E.A. Brown	s.n.	KM220226	KM220090	KM220157
NSW974474	<i>Radula sp.</i> NSW974474	E.A. Brown	s.n.	KM220228	-----	KM220159
NSW974478	<i>Radula sp.</i> NSW974478	E.A. Brown	s.n.	KM220227	KM220091	KM220158
NSW974489	<i>Radula sp.</i> NSW974478	E.A. Brown	s.n.	KM220229	KM220092	KM220160
NSW974480	<i>Radula sp.</i> NSW974481	E.A. Brown	s.n.	KM220220	KM220084	KM220151
NSW974481	<i>Radula sp.</i> NSW974481	E.A. Brown	s.n.	KM220221	KM220085	KM220152
NSW974483	<i>Radula sp.</i> NSW974481	E.A. Brown	s.n.	KM220225	KM220089	KM220156
NSW974485	<i>Radula sp.</i> NSW974485	E.A. Brown	s.n.	KM220223	KM220087	KM220154
NSW978177	<i>Radula sp.</i> NSW974485	C.D. Kilgour	939	KM220209	KM220073	KM220139

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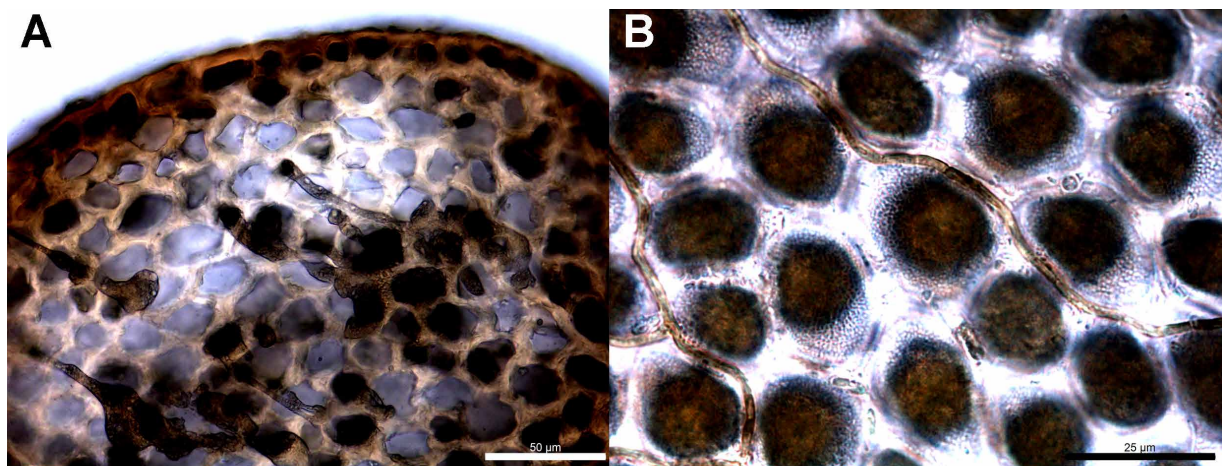


Fig. 23. *Radula decurrens* Plate B. A: Transverse section of primary stem (50 µm). B: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). Both from NSW978127.

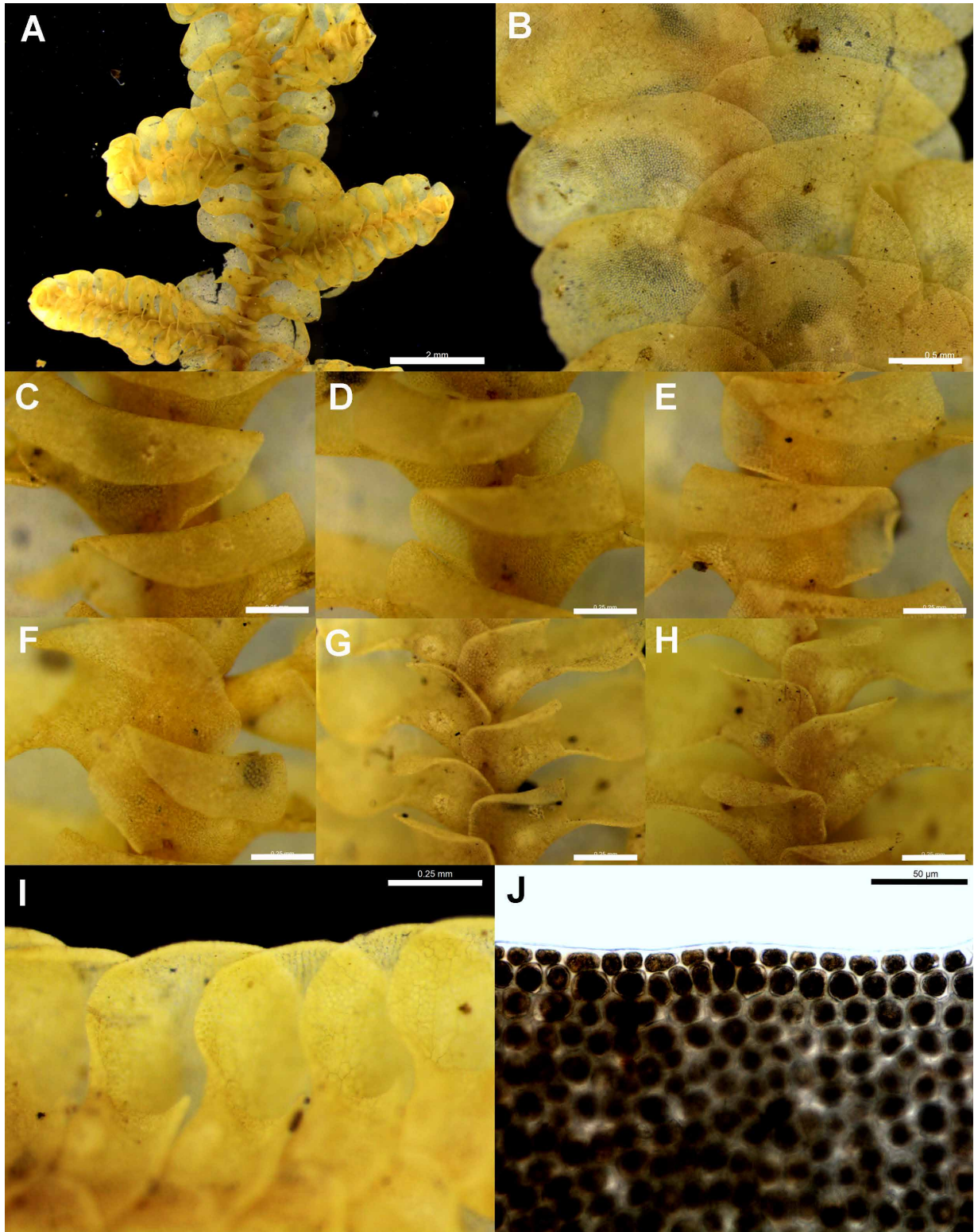


Fig. 24. *Radula decurrens* Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μm). C–E: Primary shoot lobules (250 μm). F–H: Secondary shoot lobules (250 μm). I: Secondary shoot lobe margins (250 μm). J: Leaf lobe marginal cells (50 μm). All from NSW978127.

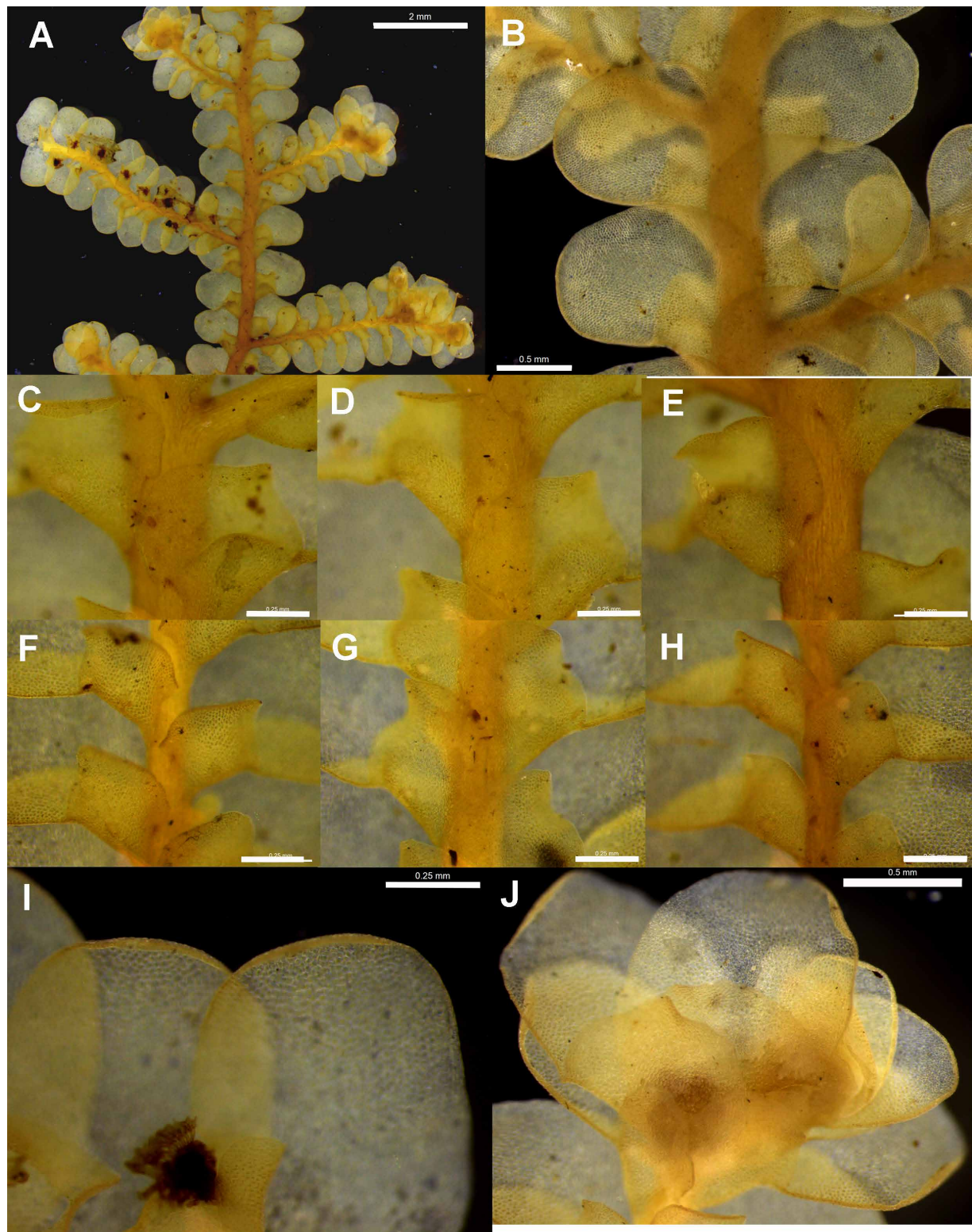


Fig. 25. *Radula oceania* Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μ m). C–E: Primary shoot lobules (250 μ m). F–H: Secondary shoot lobules (250 μ m). I: Secondary shoot lobe margins (250 μ m). J: Female bracts (500 μ m). All from NSW889516.

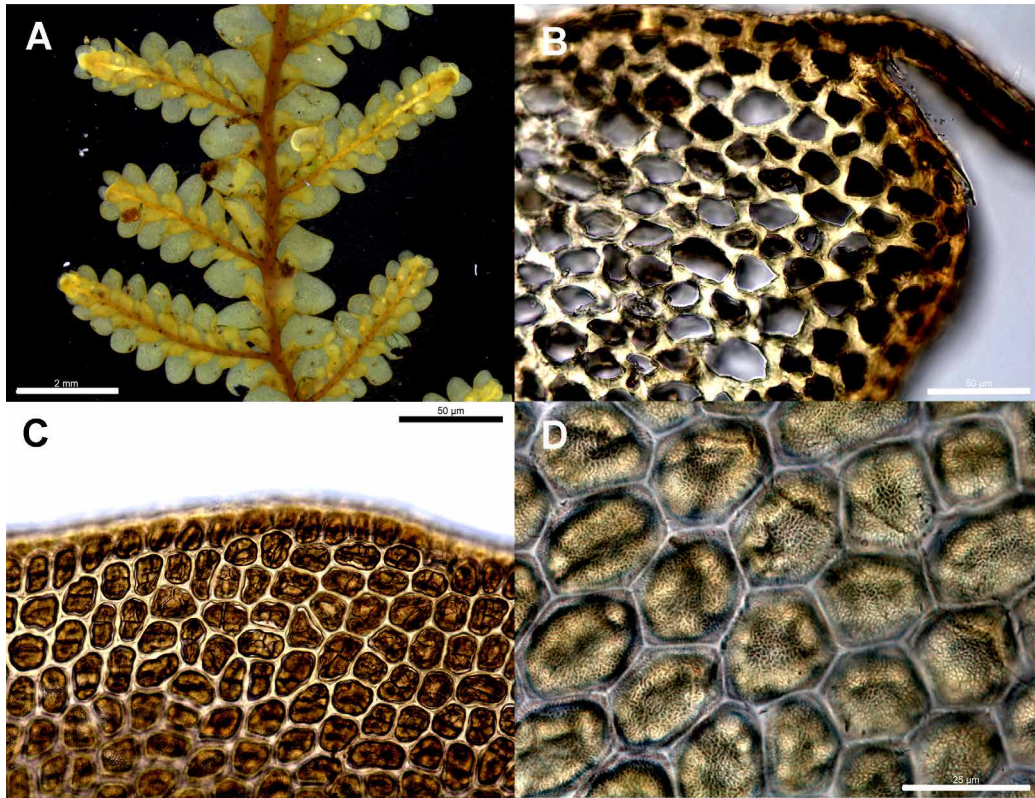


Fig. 26. *Radula oceania* Plate B. A: Ventral view of male shoot (2 mm); B: Transverse section of primary stem (50 µm). C: Cells of leaf-lobe margin, primary shoot (50 µm). D: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). A from NSW890202, B–D from NSW889516.

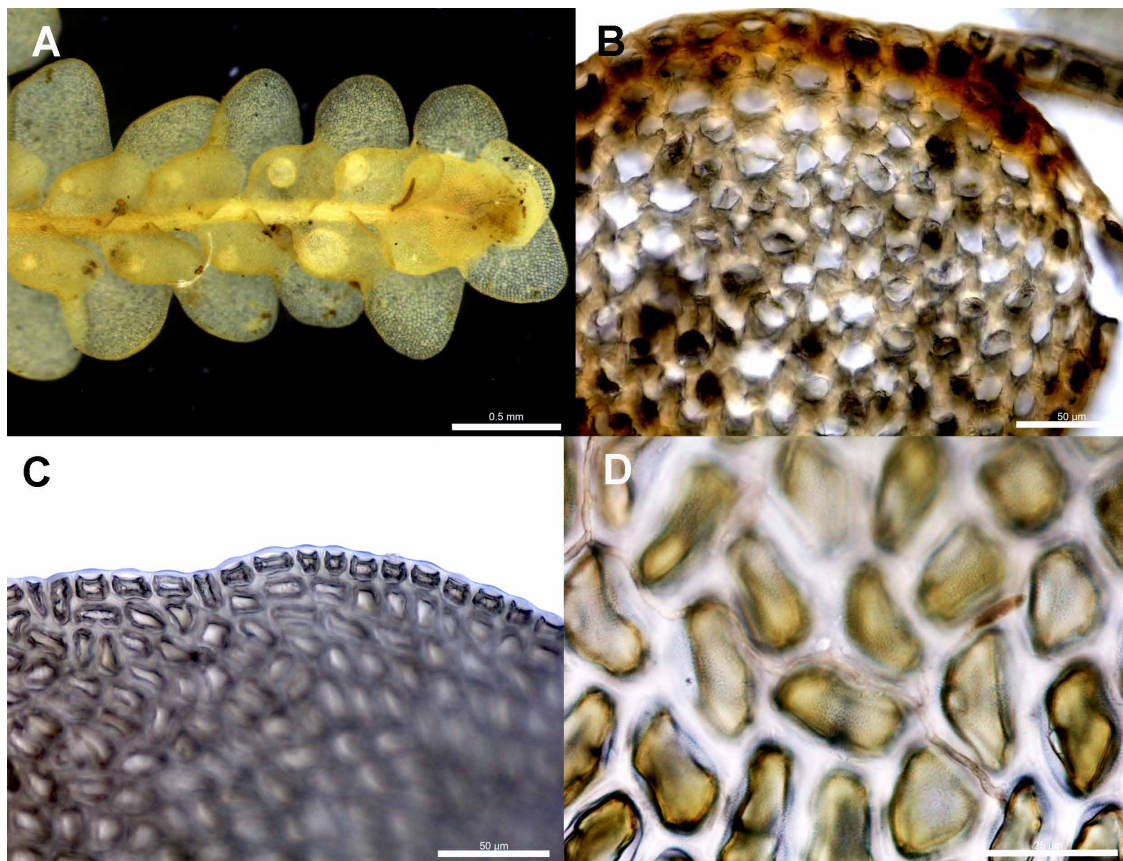


Fig. 27. *Radula* sp. NSW974474 Plate B. A: Male bracts on secondary branch (500 µm). B: Transverse section of primary stem (50 µm). C: Cells of leaf-lobe margin, primary shoot (50 µm). D: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). A from NSW890202, B–D from NSW974474.

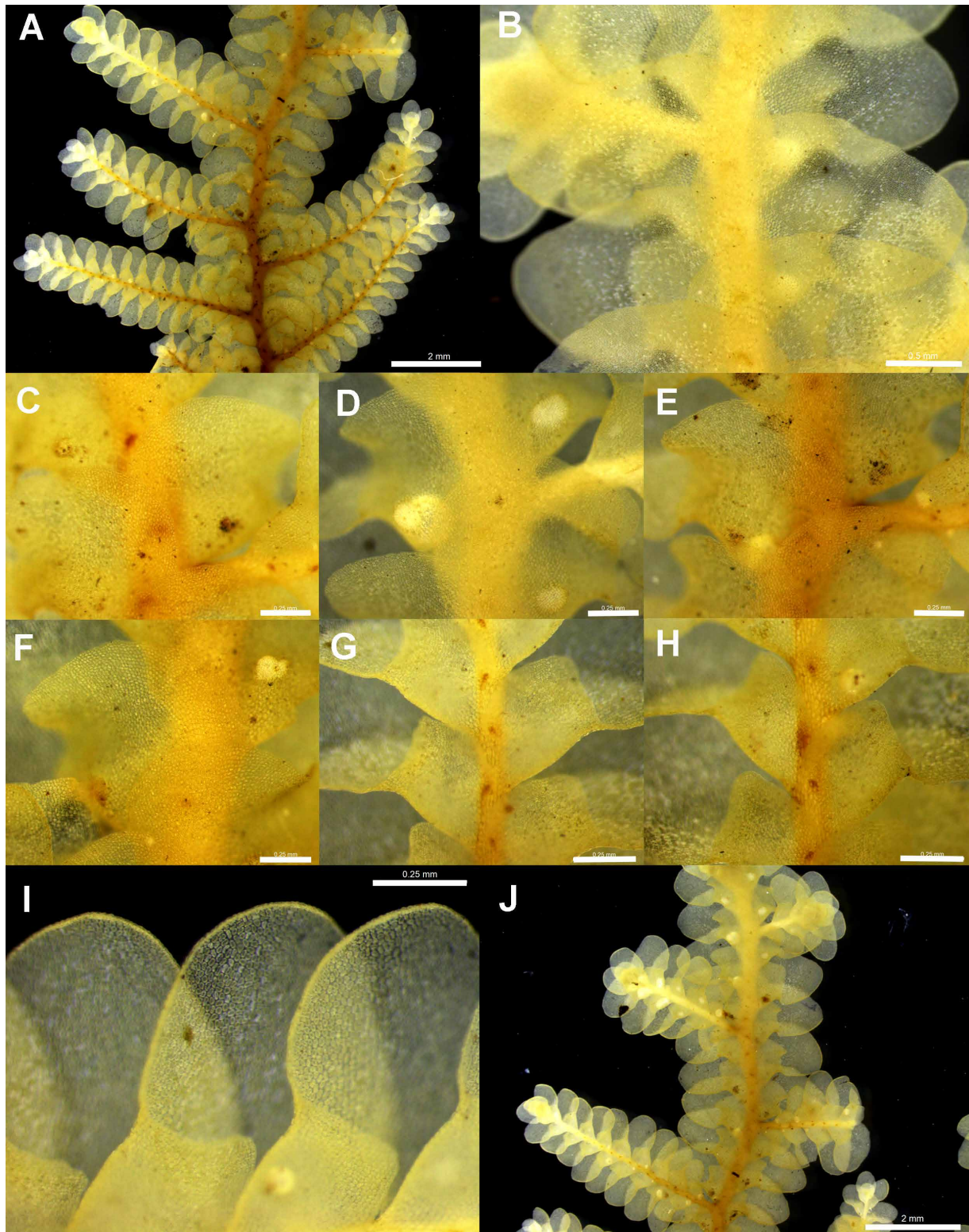


Fig. 28. *Radula* sp. NSW974474 Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μ m). C–E: Primary shoot lobules (250 μ m). F–H: Secondary shoot lobules (250 μ m). I: Secondary shoot lobe margins (250 μ m). J: Ventral view of primary shoot (2 mm). All from NSW974474.

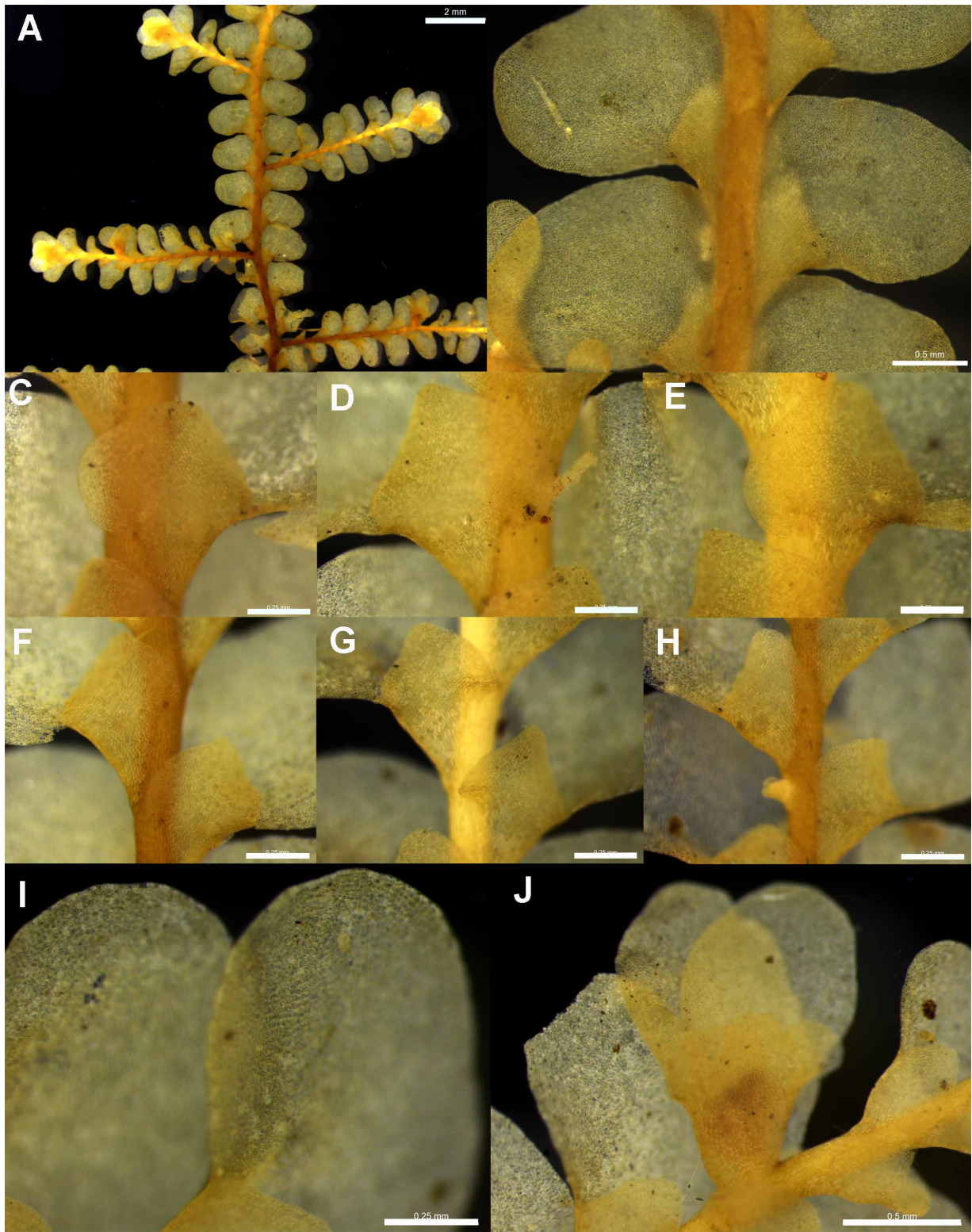


Fig. 29. *Radula* sp. NSW974478 Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μm). C–E: Primary shoot lobules (250 μm). F–H: Secondary shoot lobules (250 μm). I: Secondary shoot lobe margins (250 μm). J: Female bracts (500 μm). All from NSW974478.

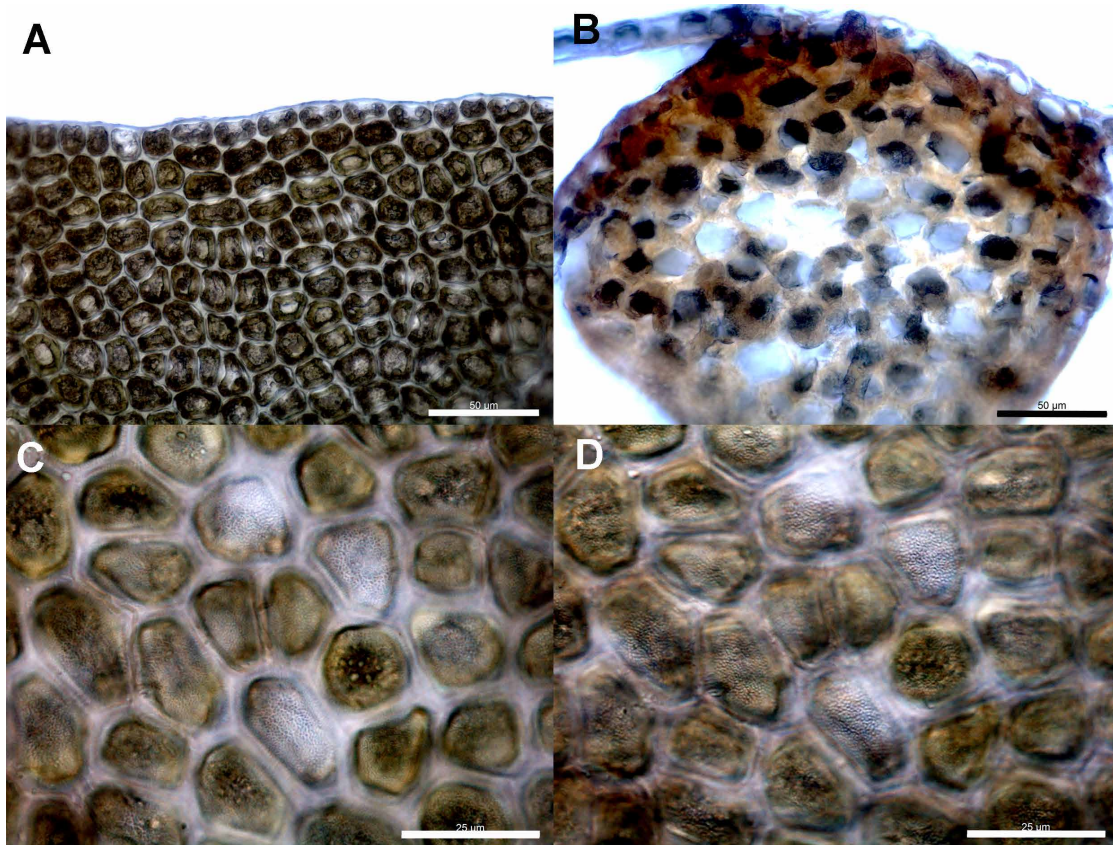


Fig. 30. *Radula* sp. NSW974478 Plate B. A: Leaf-lobe margin (50 µm). B: Transverse section of primary stem (50 µm). C, D: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). All from NSW974478.

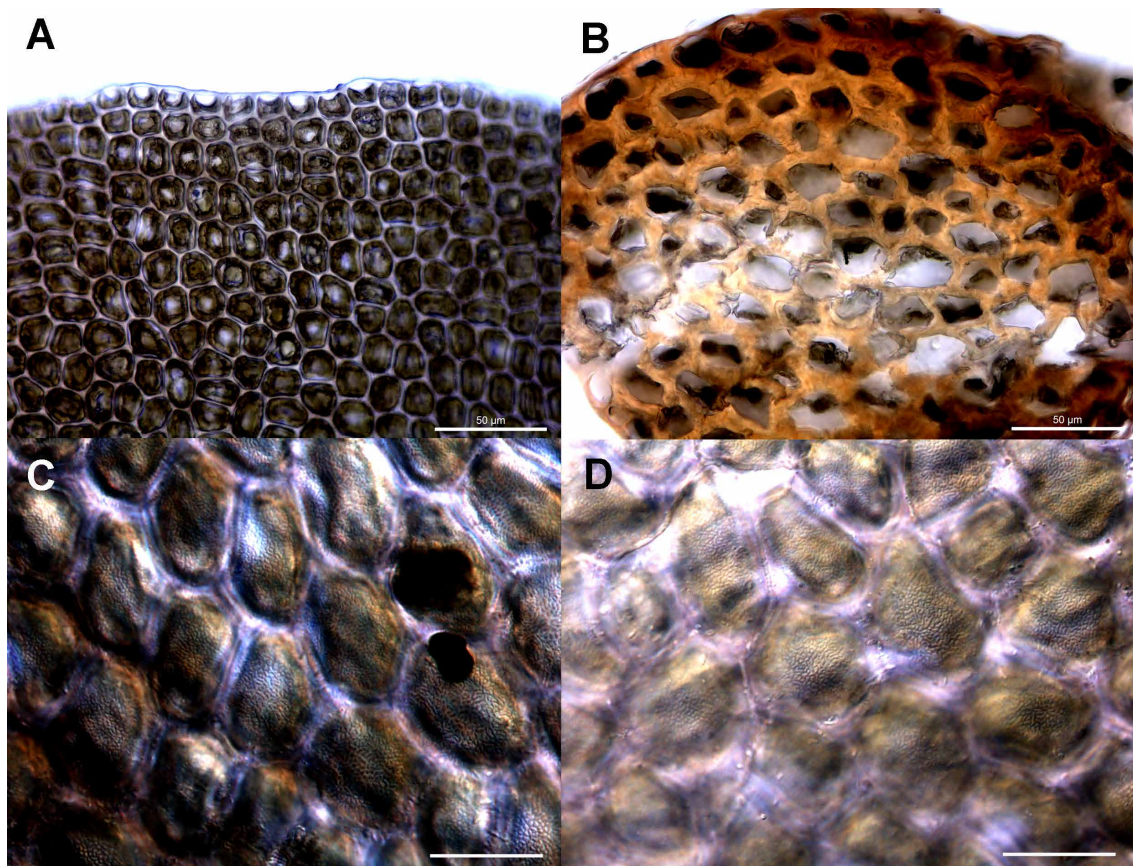


Fig. 31. *Radula* sp. NSW974485 Plate B. A: Leaf-lobe margin (50 µm). B: Transverse section of primary stem (50 µm). C, D: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). From NSW974485.

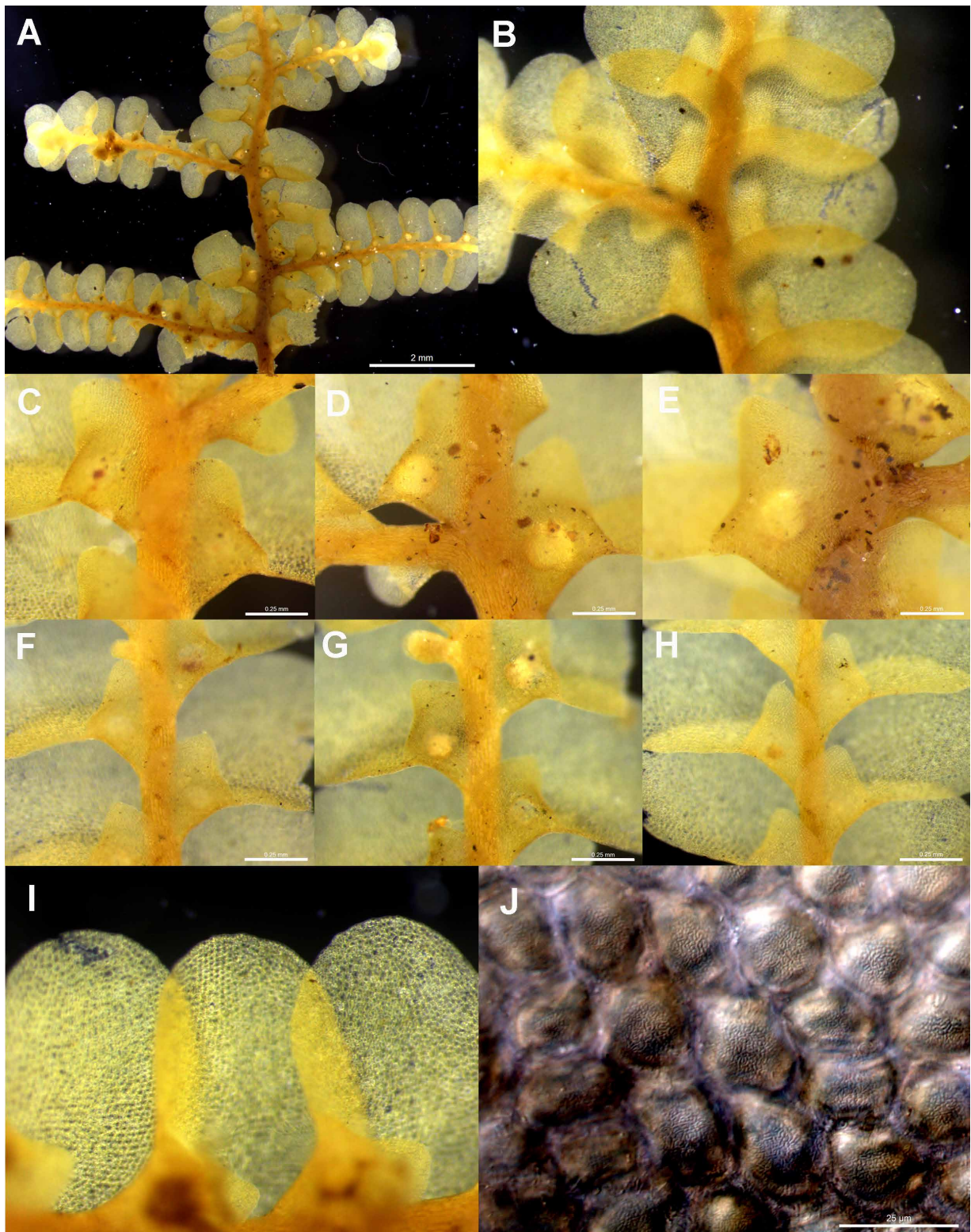


Fig. 32. *Radula* sp. NSW974485 Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 µm). C–E: Primary shoot lobules (250 µm). F–H: Secondary shoot lobules (250 µm). I: Secondary shoot lobe margins (250 µm). J: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). From NSW974485.

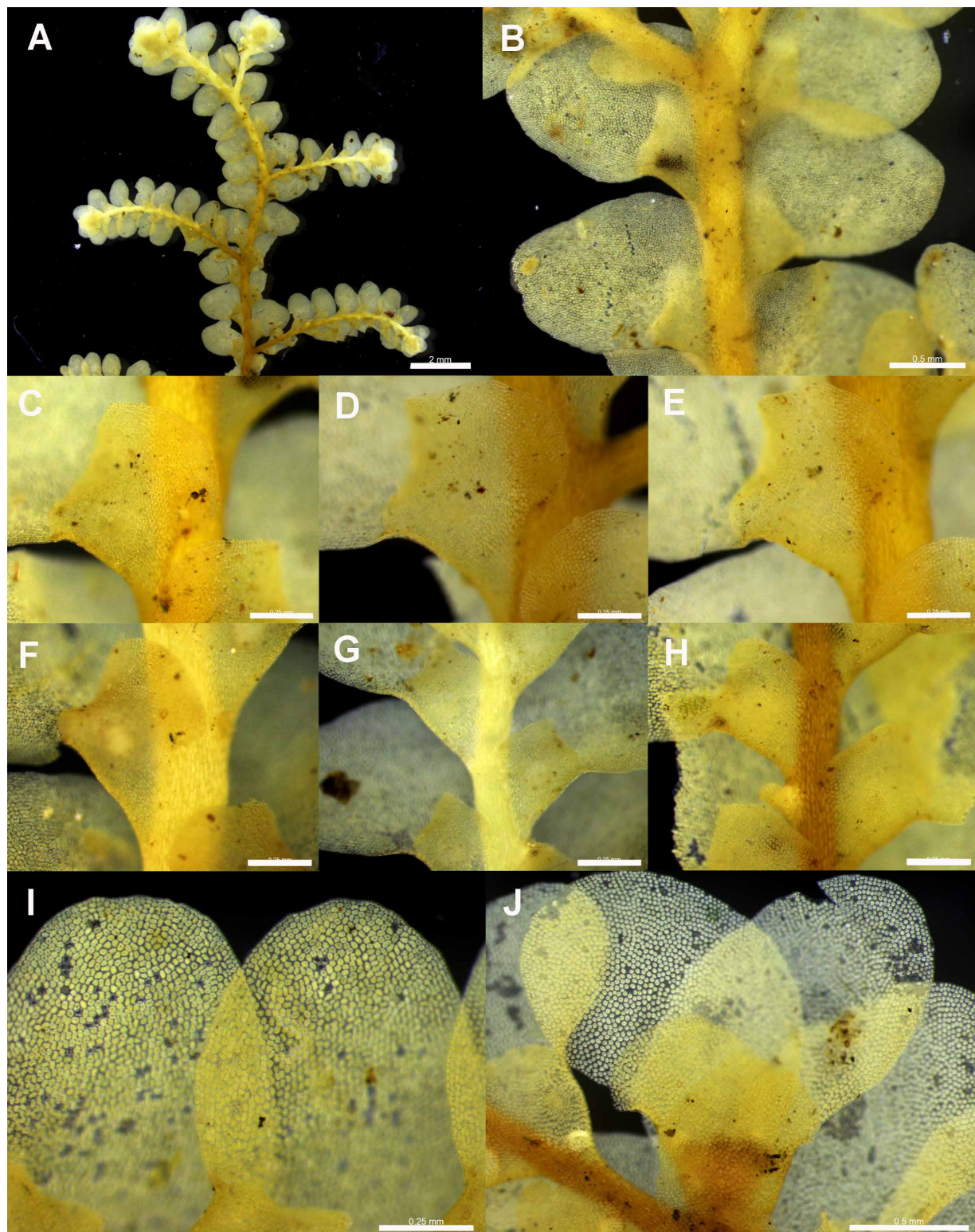


Fig. 33. *Radula* sp. NSW973452 Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 µm). C–E: Primary shoot lobules (250 µm). F–H: Secondary shoot lobules (250 µm). I: Secondary shoot lobe margins (250 µm). J: Female bracts (500 µm). All from NSW973452.

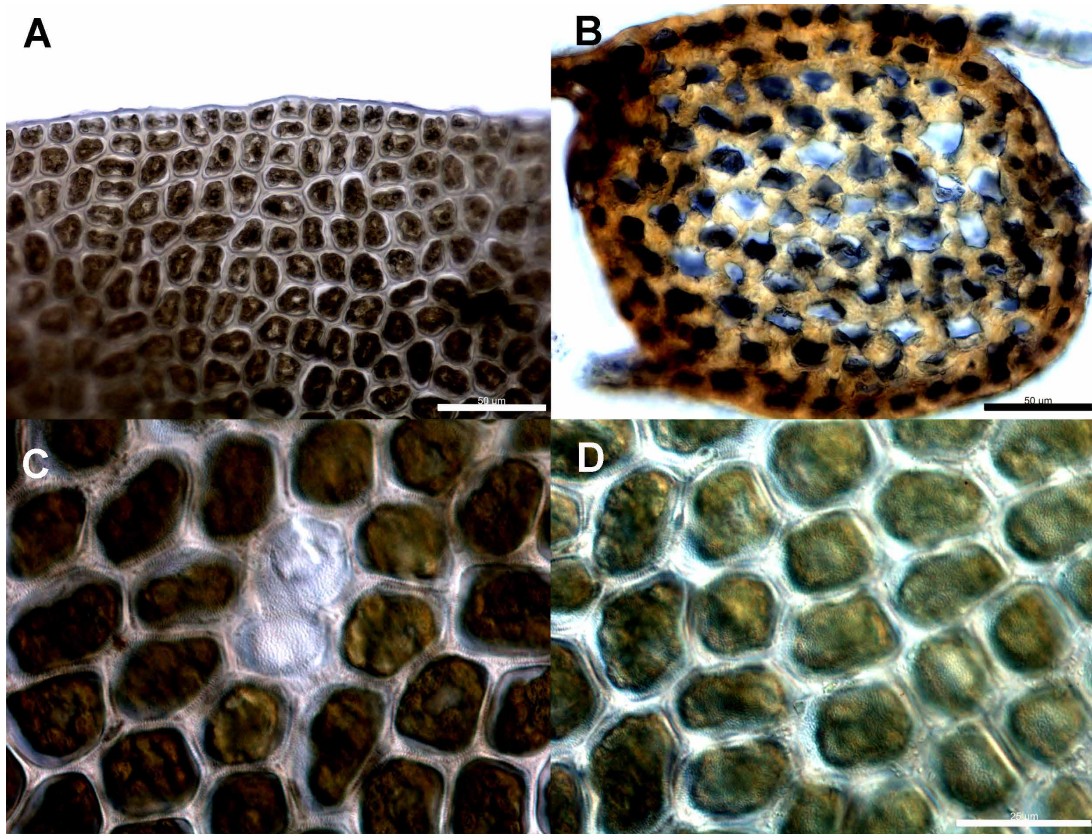


Fig. 34. *Radula* sp. NSW973452 Plate B. A: Leaf-lobe margin (50 µm). B: Transverse section of primary stem (50 µm). C, D: Leaf-lobe medial cell surface, showing rugose ornamentation (25 µm). From NSW973452.

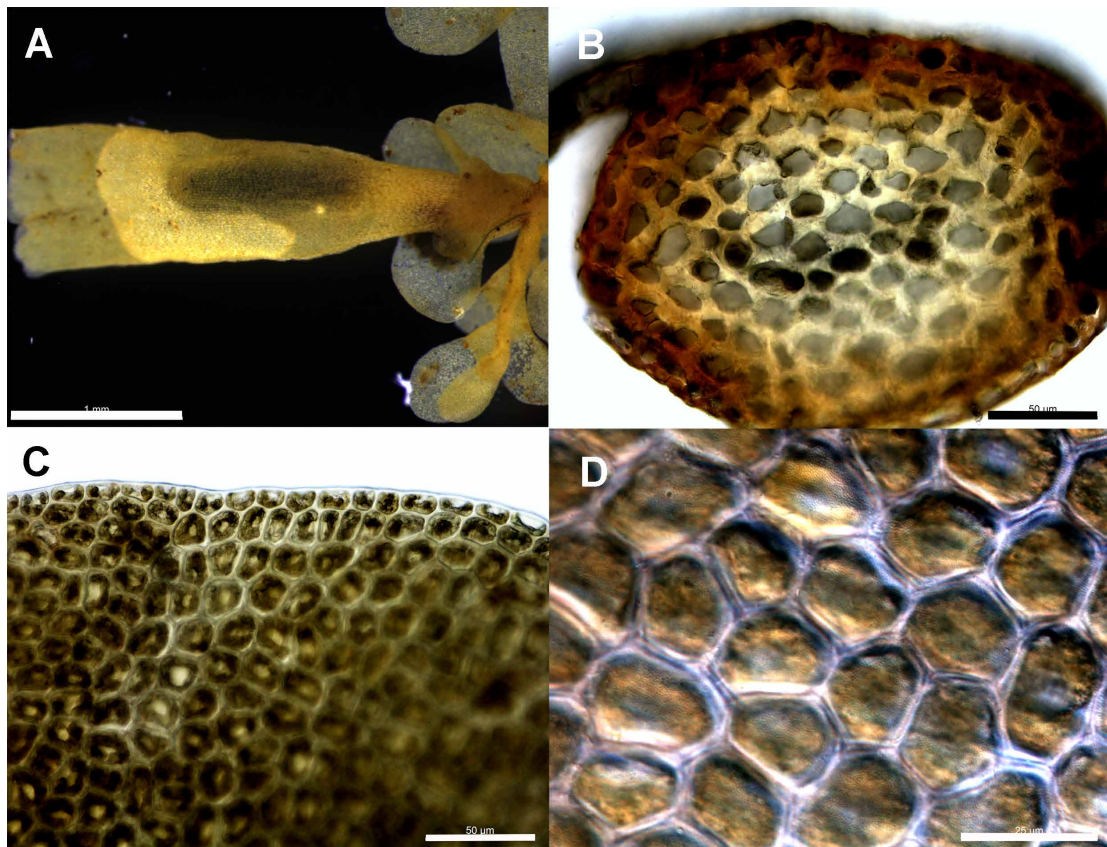


Fig. 35. *Radula* sp. NSW895234 Plate B. A: Ventral view of perianth (1 mm). B: Transverse section of primary stem (50 µm). C: Leaf-lobe margin (50 µm). D: Leaf-lobe medial cell surface, showing faint rugose ornamentation (25 µm). All from NSW895234.

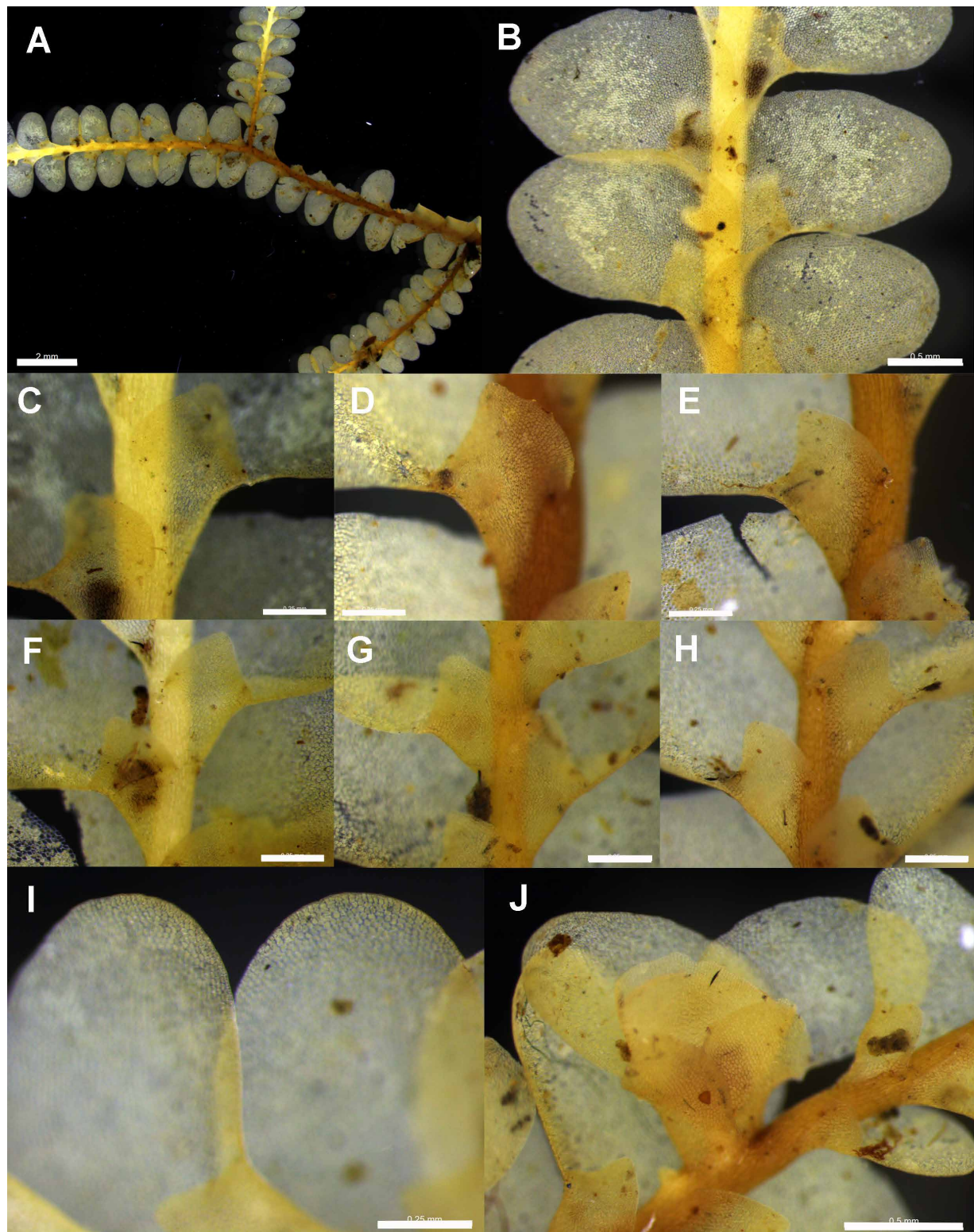


Fig. 36. *Radula* sp. NSW895234 Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μ m). C–E: Primary shoot lobules (250 μ m). F–H: Secondary shoot lobules (250 μ m). I: Secondary shoot lobe margins (250 μ m). J: Female bracts (500 μ m). All from NSW895234.

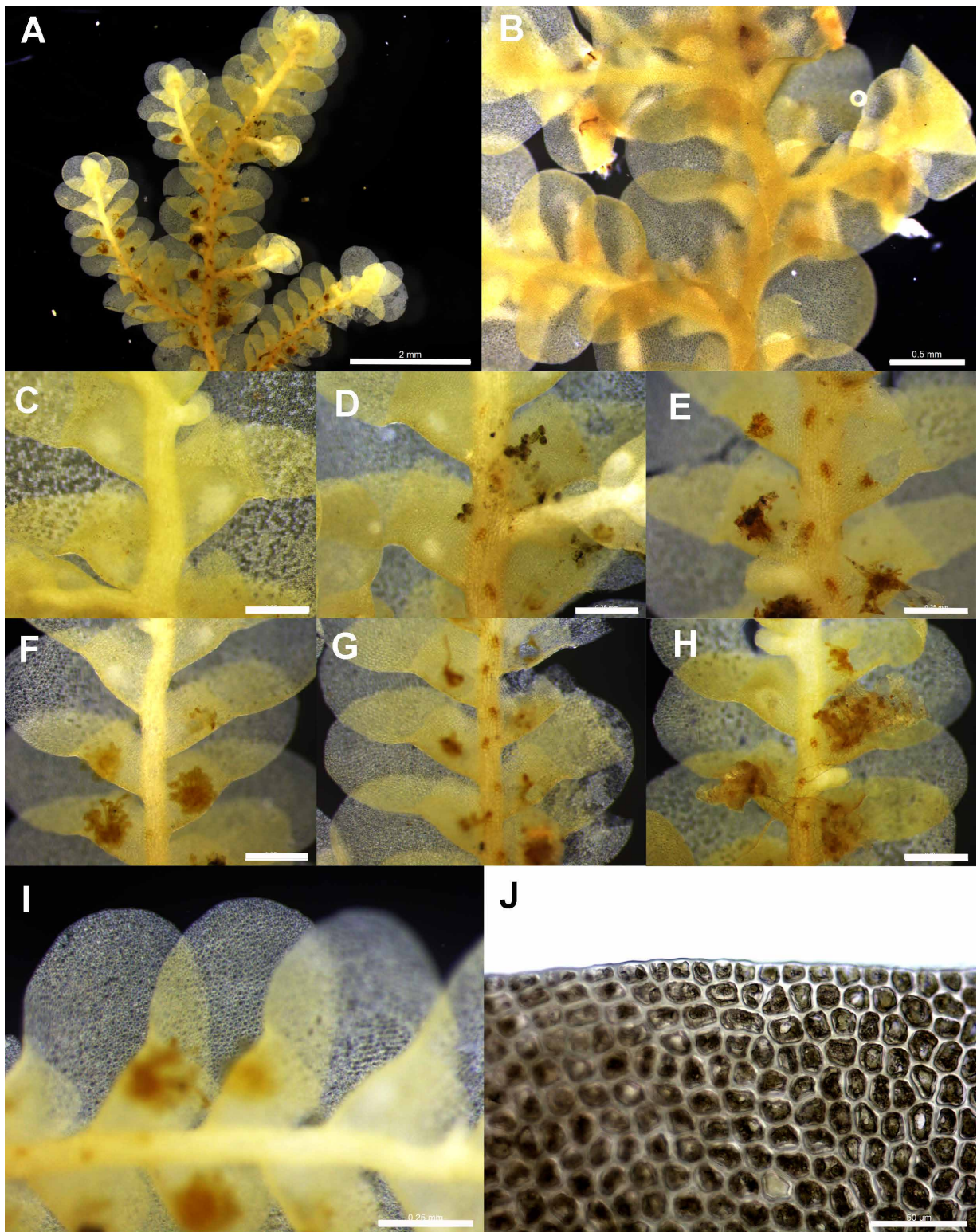


Fig. 37. *Radula* sp. NSW974481 Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 μm). C–E: Primary shoot lobules (250 μm). F–H: Secondary shoot lobules (250 μm). I: Secondary shoot lobe margins (250 μm). J: Cells of leaf-lobe margin, primary shoot (50 μm). All from NSW974481.

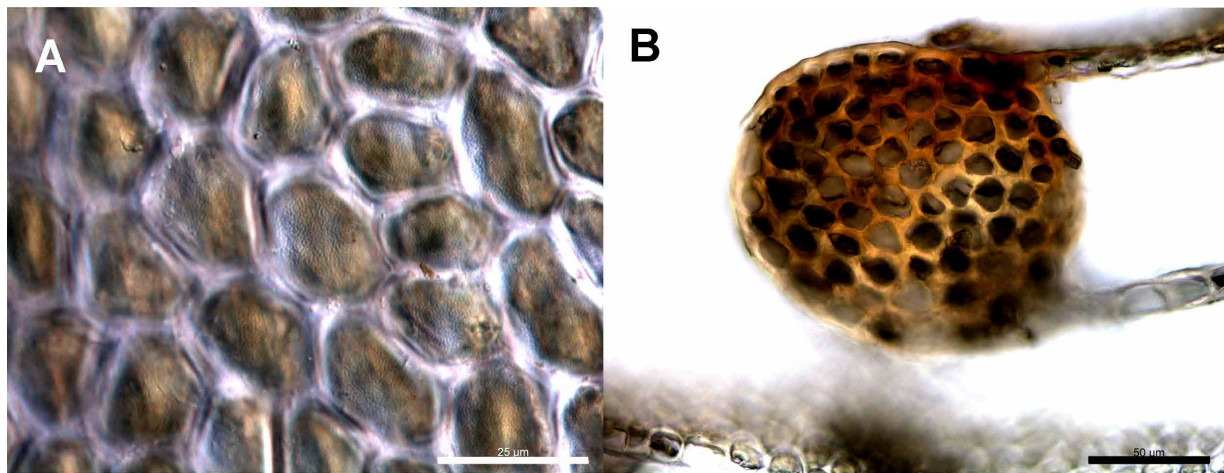


Fig. 38. *Radula* sp. NSW974481 Plate B. A: Leaf-lobe medial cell surface, showing rugose ornamentation (25 μm). B: Transverse section of primary stem (50 μm). Both from NSW974481.

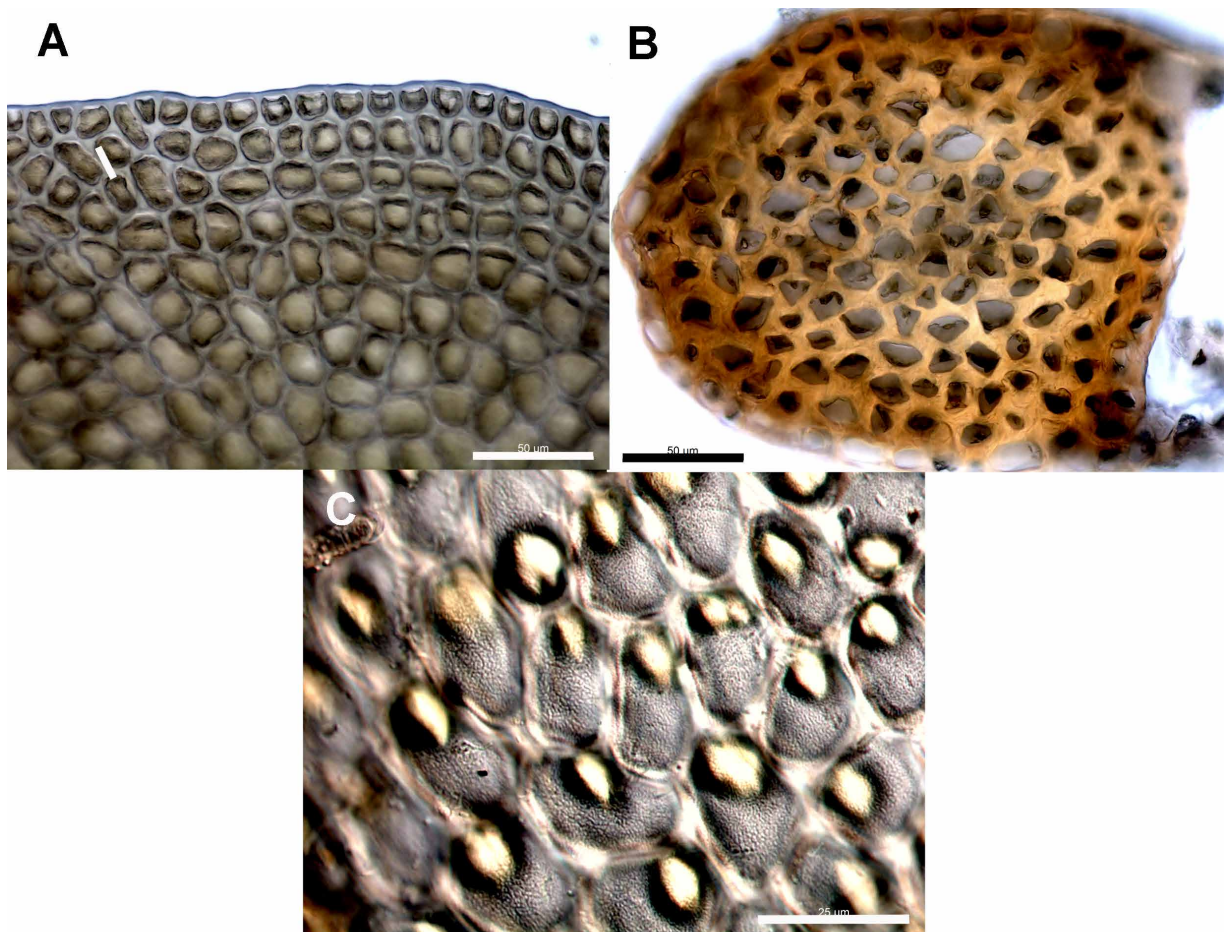


Fig. 39. *Radula* sp. NSW974317 Plate B. A: Leaf-lobe margin (50 μm). B: Transverse section of primary stem (50 μm). C: Leaf-lobe medial cell surface, showing rugose ornamentation (25 μm).

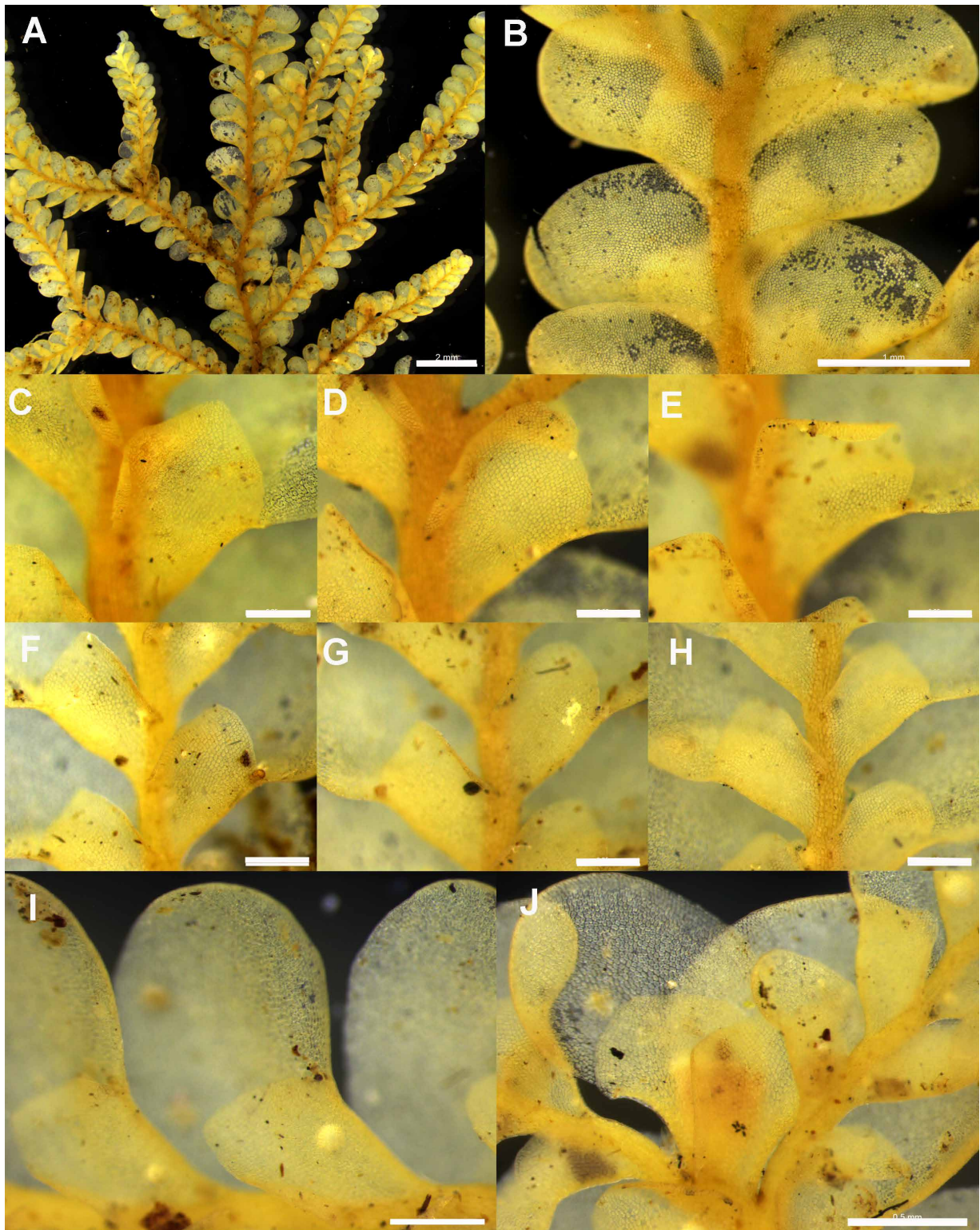


Fig. 40. *Radula* sp. NSW974317 Plate A. A: Ventral view of primary shoot (2 mm). B: Dorsal view of primary shoot (500 µm). C–E: Primary shoot lobules (250 µm). F–H: Secondary shoot lobules (250 µm). I: Secondary shoot lobe margins (250 µm). J: Female bracts (500 µm). All from NSW974317.

Appendix 1: Additional species included in molecular phylogeny.

***Radula decurrens* Mitt. *Flora Vitiensis*: 419. 1871 [1873]**

Type: Samoa Island. T. Powell s.n. NY!

Figs 23–24.

Specimens examined: FIJI: VITI LEVU: west of Namosi Village, 18° 3' 3" S 178° 7' 9" E, 130 m, 30 Aug 2011, L. Söderström 2011/056, M. von Konrat et al. (NSW978127).

***Radula oceania* Castle *Cryptogamie, Bryologie, Lichénologie* 5: 390. 1965**

Type: Samoa, *Rechinger*, No. 3359, as *R. multiflora* G., in Hb. Steph. (Holotype: G00046045 (G-15116)!)

Figs 25–26.

Specimens examined: FIJI: VITI LEVU: Naitasira District, Ulvi Nakoba, vicinity of transmission station at summit, 18° 03' 38" S 178° 25' 00" E, 460 m, 29 Aug 2011, M.A.M. Renner 5332 et al. (F; NSW889321; SUVA); Rairaimatuku Plateau, Monasavu, on road to Tominivi, 17° 43' 31" S 178° 2' 15" E, c. 900 m, 4 Sep 2011, M.A.M. Renner 5571 et al. (EGR; F; NSW895198; SUVA); M.A.M. Renner 5578 et al. (NSW895229); Southern sector of Namosi Road, 18° 04' 58" S 178° 09' 44" E, 530 m, 31 Aug 2011, M.A.M. Renner 5412 et al. (F; NSW889516; SUVA); Nabukelevu mountain above Nadakuni Village and between Waiaboa Stream and Sovi Basin, 17° 56' 59" S 178° 16' 16" E, 720–750 m, 1 Sep 2011, M.A.M. Renner 5493, M.J. von Konrat & F. Rakoro (F; NSW890182; SUVA); Kadavu: Nabukelevu-Ira Village lands, Nabukelevu Mountain, Able's track to summit from village, 650–800 m, 19° 07' 16" S 177° 58' 37" E, M.A.M. Renner 5721 et al. (NSW974316).

***Radula* sp. NSW974474**

Figs 27–28

Specimens examined: VANUATU: Sanma, E of Penaraou, S of Logmoli airstrip, Espiritu Santo, 14° 58' S 166° 39' S, 1200 m, Nov 2006, E.A. Brown s.n. (NSW974472, 974474).

FIJI: VITI LEVU: Rairaimatuku Plateau, on a summit with telecommunication tower, 16 km S of Monasavu, 17° 47' 31" S 178° 01' 14" E, 1265 m, 03 Sep 2011, M.A.M. Renner 5522 et al. (NSW890202; F); M.A.M. Renner 5570 et al. (NSW895197; F; SUVA).

***Radula* sp. NSW974478**

Figs 29–30

Representative specimens examined: VANUATU: Sanma, E of Penaraou, S of Logmoli airstrip, Espiritu Santo, 14° 21' 49" S 166° 32' 53" E, 600 m, Nov 2006, E.A. Brown s.n. (NSW974478, 974489).

***Radula* sp. NSW974485**

Figs 31–32

Specimens examined: VANUATU: Sanma, E of Penaraou, S of Logmoli airstrip, Espiritu Santo, 14° 21' 49" S 166° 32' 53" E, 600 m, Nov 2006, E.A. Brown s.n. (NSW974485).

MALAYSIA: SABAH: Kinabalu National Park, C.D. Kilgour 939 (NSW978177; SNP).

***Radula* sp. NSW973452**

Figs 33–34.

Specimens examined: FIJI: Kadavu Island: Nabukelevu-Ira Village, Nabukelevu mountain, north-western edge of summit crater, 19° 07' 06" S 177° 58' 48" E, 800 m, 9 Sep 2011, M.A.M. Renner 5767 et al. (F; NSW895644); M.A.M. Renner 5782 et al. (NSW978103; SUVA); Nabukelevu-Ira Village, Nabukelevu Mountain, Able's track to summit from village, 19° 7' 16" S 177° 58' 37" E, 650 m, 9 Sep 2011, M.A.M. Renner 5732 et al. (NSW973452; SUVA).

***Radula* sp. NSW895234**

Figs 35–36.

Specimens examined: FIJI: VITI LEVU: Rairaimatuku Plateau, Monasavu, on road to Tominivi, 17° 43' 31" S 178° 2' 15" E, 1150–1200 m, 4 Sep 2011, M.A.M. Renner 5583 et al. (F; NSW895234; SUVA); M.A.M. Renner 5577 et al. (F; NSW895228; SUVA).

***Radula* sp. NSW974481**

Figs 37–38.

Specimens examined: VANUATU: Sanma, E of Penaraou, S of Logmoli airstrip, Espiriu Santo, 14° 21' 49" S 166° 32' 53" E, 600 m, 13 Nov 2006, *E.A. Brown s.n.* (NSW974480, NSW974481, NSW974483).

***Radula* sp. NSW974317**

Figs 39–40.

Specimens examined: FIJI: Kadavu, Nabukelevu-Ira Village, Nabukelevu Mountain, Able's track to summit from village up WSW side of mountain, 19° 7' 16" S 177° 58' 37" E, 650–800 m, 9 Sep 2011, *M.A.M. Renner 5717 et al.* (NSW974317; SUVA); Kadavu, S of Vunisea of Tavuki (Vunisea-Namara) Road, 19° 4' S 178° 10' E, 150 m, 7 Sep 2011, *M.A.M. Renner et al. 5691* (NSW978178; SUVA).

***Radula* sp. NSW889416**

Specimen examined: FIJI: VITI LEVU: Naitasiri District, Ulvi Nakoba, vicinity of transmission station at summit, 18° 3' 38" S 178° 25' 0" E, 460 m, 30 Aug 2011, *M.A.M. Renner 5373 et al.* (F; NSW889416; SUVA).

